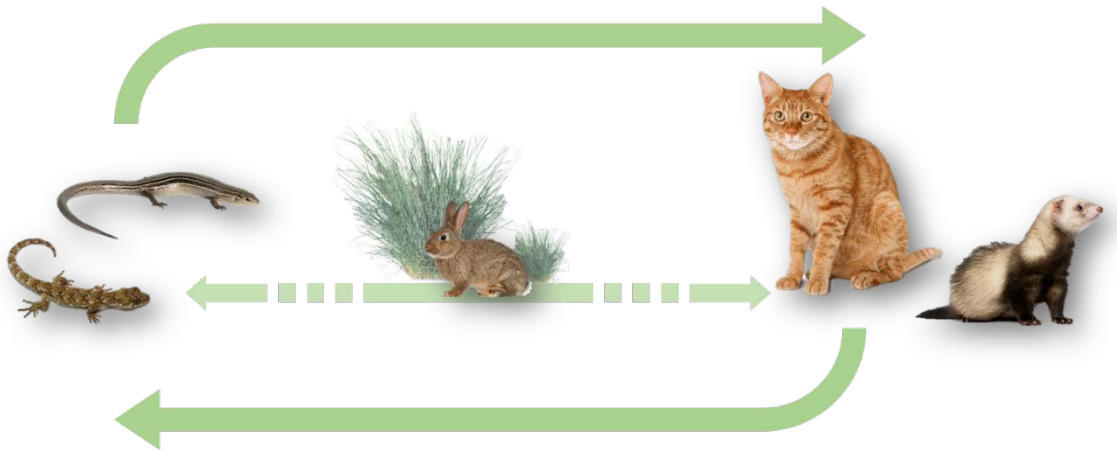
Interactions between native lizards and introduced mammals in New Zealand's dryland ecosystems



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Master of Science (Biological Sciences)

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DECLARATIONS

Declaration of Originality

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Statement of Ethical Conduct

The study methods and data collection for chapter 2 were approved by the University of Tasmania Animal Ethics Committee (ref: A0016869), the Manaaki Whenua – Landcare Research Animal Ethics Committee (ref: 17/09/01) and the New Zealand Department of Conservation (permit ref: 61099-CAP).

The study methods and data collection for chapter 3 were approved by the Manaaki Whenua – Landcare Research Animal Ethics Committee (ref: 94/4/8).

The research associated with this thesis abides by the international and Australian codes on human and animal experimentation and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University.

Signature

Dated: 7 June 2019

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ABSTRACT

Introduced predators have had devastating impacts for native prey globally, contributing to high rates of species extinction and endangerment, particularly within island ecosystems. New Zealand is one of these island systems where native fauna, including a high diversity of endemic lizard species, are highly threatened. The heightened vulnerability of New Zealand's fauna to introduced predators is often attributed to prey-naivety, which results from a lack of experience with mammalian predators over evolutionary time-scales. In addition to introduced predators, New Zealand's native species are threatened by habitat degradation, introduced prey species, and synergies between these co-occurring threats.

Effective conservation in heavily modified ecosystems with multiple invaders is an ongoing challenge globally, with management actions often having unintended consequences. Understanding the interactions between native lizards and introduced mammalian predators, is therefore essential to ensuring New Zealand's biodiversity is conserved effectively and efficiently. This study focused on understanding the extent to which two key threats; (i) prey naivety and (ii) hyperpredation, contribute to the heightened vulnerability of lizards in New Zealand's dry grassland habitats (drylands). This included assessing how current conservation management strategies, including (i) mammalian-predator exclusion and (ii) rabbit control, were impacting lizard populations.

The first aim of the study is to understand the extent to which New Zealand lizards remain naïve of the threat posed by introduced mammalian predators. To do this we tested whether McCann's skink (*Oligosoma maccanni*), a 'non-threatened' dryland lizard species, responded to cat cues by reducing basking frequency or increasing their preference for basking sites closer to refuge. We found that skinks from a population with a high-density of introduced mammals reduced basking frequency when exposed to cat cues, whereas skinks from a low-predator population, sourced from within a fenced reserve where mammalian predators had been excluded for 3-4 skink generations, did not. The low-predator population also failed to discriminate the cues of an avian predator, despite having evolutionary and ecological experience with this predatory threat. These results suggest that at least one species of New Zealand lizard has rapidly gained the ability to recognise the threat posed cats, a species

introduced ~150 years ago. However, they also suggest that the behavioural response of skinks is flexible, and that predator avoidance behaviours can be rapidly lost when predation pressure is relaxed.

The second aim is to better understand if and how an introduced prey species, in this case rabbits (*Oryctolagus cuniculus*), facilitates hyperpredation of native prey. Hyperpredation occurs when rabbits support higher densities of a shared generalist predator, which increases predation pressure on alternative prey species, particularly when rabbits become less abundant. Specifically, we are interested in whether rabbit control is an effective mechanism for reducing the impacts of ferret (*Mustela furo*) predation on native lizards and invertebrates in New Zealand's drylands. To do this we analysed changes in ferret densities and per-capita dietary intake in response to a large-scale rabbit control operation, in the period up to 18 months post-control. Following rabbit control, ferret densities declined but remaining ferrets increased their per capita consumption of native prey. This resulted in an overall decrease in predation pressure for invertebrates, but an increase in predation pressure for lizards. These results indicate that reducing rabbits by over 80% in this system fails to protect lizards in the short-term period following rabbit-control, and that lizard conservation would benefit from the simultaneous control of predators.

This research demonstrates that prey-naivety is dynamic, and that evolutionary isolation from mammalian predators does not prevent New Zealand's lizards from recognising and attempting to avoid the risk associated with novel predator cues. This research also highlights how established rabbit populations and short-term fluctuations in rabbit abundance, increase native species' vulnerability to introduced predators. Finally, this research demonstrates that current management strategies aimed at protecting vulnerable native species, can have unintended consequences. This includes increasing the naivety of prey through conservation fencing and predator exclusion, as well as increasing the predation pressure on native prey species through suppressing introduced prey populations**.** To understand the vulnerability of native species, and ensure to conservation actions are effective, research must continue to unravel the spatial and temporal complexity of species interactions within invaded ecosystems.

PHOTO ESSAY OF STUDY AREA, SPECIES AND METHODS

These photos are presented to help the reader understand the landscape, species and methods involved in this project.

Dryland landscapes have been heavily modified by human activity, and now often exist in a mosaic with pastural land for grazing sheep (photo: Unknown).

Dryland ecosystems are home to a diverse range of lizard species, the majority of which are threatened. This includes the Otago Skink (*Oligosoma otagense*) currently classed as 'nationally endangered' (L), and the Jewelled gecko (*Naultinus gemmeus*) currently classed as 'at risk' (R) (photos: Andrew Blayney).

Dryland ecosystems have large numbers of introduced mammalian predators including feral cats, mustelids and hedgehogs, as well as highly abundant rabbits (photos: Hannah Cliff).

Numerous conservation fences have been constructed to protect threatened lizard species by excluding mammalian predators. Skinks from within this fence at Macraes Flat, an area which is managed by the New Zealand Department of Conservation (DOC) and has been free of all mammalian predators since August 2006, were used for behavioural trials (photo: Grant Norbury).

To investigate the extent to which New Zealand lizards are threatened by predation because of prey naivety, I tested whether McCann's skinks (*Oligosoma maccanni*), a 'non-threatened' and commonly occurring dryland lizard species, could discriminate the cues of introduced and coevolved predators (photo: Robert Atkinson).

To test predator recognition, 64 skinks were caught in the field and brought into a controlled laboratory setting for behavioural trials. Testing occurred in arenas containing basking and refuge sites (photo: Hannah Cliff).

I assessed skinks response to predator cues by analysing camera trap photos that captured the basking behaviour of individually marked skinks (photo: Hannah Cliff).

Introduced rabbits are frequently controlled in dryland ecosystems by distributing poison baits, shooting, and viral releases (e.g. rabbit haemorrhagic disease virus). Changes in rabbit density have flow-on effects to other dryland species, including predators which consume rabbits as their primary prey source and alternative prey species, including native lizards, invertebrates and birds. (photo: New Zealand Geographic, accessed online: https://www.nzgeo.com/wp-content/uploads/2016/04/ 139_BunnyHunt 11-1600x1066.jpg)

Introduced ferrets are a key predatory threat to native prey in dryland ecosystems. Ferret abundance is largely driven by 'bottom-up' processes, including the abundance of their primary prey – rabbits. By trapping ferrets before and after a large-scale rabbit baiting operation, it was possible to measure the numerical response of ferrets to changes in rabbit abundance (Photo: Grant Norbury).

In addition to rabbits, ferrets regularly consume large numbers of alternative prey, including lizards. I analysed how ferret diet was affected by rabbit control by using data collected from trapped ferret's scats, which quantified the number of individual prey items ferrets consumed. In one instance a single scat contained 19 individual lizards (photo: Richard Heyward).

CONTENTS

CHAPTER 1

General Introduction

1.1 Impacts of introduced predators in island systems

Introduced predators, and particularly introduced mammalian predators, are a major threat to global biodiversity (Doherty et al. 2016). The impacts of introduced mammalian predators have been especially severe on islands, where they have contributed to disproportionately high rates of species extinction and endangerment (Case and Bolger 1991, Doherty et al. 2016, Spatz et al. 2017). Invasive mammalian predators have been linked to 58% of modern bird, mammal or reptile extinctions (142 species), 87% of these extinctions being island endemic fauna. Invasive mammalian predators threaten a further 596 bird, mammal or reptile species, 80% of which are island species (Doherty et al. 2016). Given that island systems are typified by reduced diversity of predators over evolutionary time-scales, island species often lack predator experience that is relevant or transferrable when defending themselves against a novel invader. As a result, insular prey species are frequently naïve, with morphologies, life-history, and/or behavioural traits that make them vulnerable to predators (Cox and Lima 2006, Tershy et al. 2015). Prey naivety heightens the risk and impacts of introduced predators on native prey. A recent meta-analysis found that the impacts of introduced predators on native prey were double that of native predators, as measured through the reductions predators imparted on prey population size and reproductive output (Salo et al. 2007).

1.2 The evolutionary history of New Zealand

The islands of New Zealand are part of the mostly submerged continent of Zealandia, which also includes New Caledonia, and numerous smaller islands (e.g. Lord Howe and Norfolk Islands). Zealandia separated from the Gondwanan supercontinent approximately 82 Ma ago (Wallis and Trewick 2009). While this separation isolated a subset of Gondwanan lineages, the extent to which New Zealand's current biodiversity originates from this initial vicariance ('Moa's Ark' sensu Bellamy et al. 1990), or from long-distance dispersal events within the last 23 Ma, remains debated (Landis et al. 2008, Giribet and Boyer 2010, Phillips et al. 2010). In any case, long periods of terrestrial isolation and evolutionary radiations resulted in very high rates of species endemism, and New Zealand's native fauna became dominated by birds, reptiles, frogs and invertebrates (Gibbs 2006). Many of these species developed traits that

are common among island-evolved fauna but are otherwise atypical, including high rates of flightlessness, dominance of k-selected life strategies with low reproductive outputs, and examples of gigantism across birds, reptiles and invertebrates (Hoare 2006, Wallis and Trewick 2009). Critically, New Zealand's evolutionary history was marked by the near-complete absence of terrestrial mammals. When humans first arrived in New Zealand in the late 13th century (Wilmshurst et al. 2008), the terrestrial mammal fauna consisted of only three species of small insectivorous bat (King 1990). While recent fossils discoveries have revealed that New Zealand was home to additional terrestrial mammals during the mid-Miocene (16-19 Ma), including at least one species likely to have preyed on small vertebrates, these species have long become extinct (Worthy et al. 2006, Hand et al. 2018). This means that before the arrival of humans, the vast majority of New Zealand's fauna had virtually no experience with any form of mammalian predator.

1.3 History of New Zealand's species introductions

The anthropogenic transformations of New Zealand began in ca. 1280 with the arrival of Polynesians (Wilmshurst et al. 2008). Polynesian arrival meant increased burning of forests, hunting of native species (leading to the extinction of numerous species e.g. 11 species of Moa), and the introduction of two terrestrial mammals – the pacific rat or Kiore (*Rattus exulans*) and the now extinct Polynesian dog (*Canis familiaris*) (Atkinson and Cameron 1993). A second wave of environmental transformation came with the arrival of Europeans in 1769, and more extensive settlement beginning in the early 1800s. Following both intentional and accidental species introductions, New Zealand now has 31 species of introduced land mammals (King 1990), 37 'introduced and naturalised' bird species (Robertson et al. 2016), three 'introduced and naturalised' frog species (Newman et al. 2013) and one 'introduced and naturalised' reptile species (Hitchmough et al. 2016). Of the 31 extant introduced terrestrial mammals, 13 are widespread (King 1990), and eight have been found to, at least occasionally, include both birds and reptiles in their diet (Blackwell 2005).

1.4 Impacts of introduced mammalian predators in New Zealand

As in island systems elsewhere, the impacts of introduced mammalian predators in New Zealand have been severe. A recent analysis found that New Zealand has the highest proportion of threatened species globally (Bradshaw et al. 2010), and introduced predators

are frequently recognised as a major threat (e.g. Craig et al. 2000, Blackwell 2005, Innes et al. 2010, Department of Conservation 2016). New Zealand is thought to have lost 40-50% of its bird diversity following the arrival of humans. While many of the larger species are thought to have been hunted to extinction by humans, the introduction of rodents, mustelids, and cats (F*elis catus)* caused the extinction of many smaller bird species (Holdaway 1989). In addition, the most recent New Zealand threat classification system (NZTCS) placed less than 18% of New Zealand's 218 species of extant, resident and native birds in the non-threatened category (Robertson et al. 2016). In New Zealand's unique evolutionary environment, prey have developed survival strategies that have focused on the need to avoid largely visual-oriented avian predators. This can explain the evolution of cryptic colouration and secretive behaviours (e.g. a 'freeze' response) in both birds and reptiles (Elliot et al. 2001, Worthy and Holdaway 2002). While such strategies are likely to have been highly effective in the pre-human period and before the spate of introduced predators, in contemporary New Zealand environments they leave native prey vulnerable. This is because mammalian predators primarily locate prey using olfactory rather than visual cues (Hughes et al. 2010). Recognising the threat of mammalian predators, the New Zealand government and community groups have invested heavily in ridding selected offshore and mainland areas of these pests (Saunders and Norton 2001, Burns et al. 2012, Russell et al. 2015). Most recently this has included the government announcement of 'Predator Free 2050' which aims to eradicate all of New Zealand of rats, stoats and possums by 2050 (New Zealand Government 2016).

1.5 Direct impacts of introduced predators on New Zealand reptiles

While New Zealand is widely renowned for its bird diversity, it is also home to a diverse radiation of reptiles. Besides one species of Tuatara (*Sphenodon punctatus*; the last of an ancient order of reptiles), all of New Zealand's resident (non-vagrant or migratory) reptiles are skinks or geckos (collectively termed 'lizards'). Current formal classification drastically under-estimates New Zealand's extant native lizard diversity, with 57 species listed as 'taxonomically determinate' and at least 47 additional species awaiting formal classification (Hitchmough et al. 2016). Of these combined 104 species, the NZTCS lists more than 80% either as 'threatened' or 'at risk', while less than 10% are listed as 'not threatened'. While local extinction is common, recorded global extinctions have so far been limited to two

species of New Zealand reptile (Kawekaweau – *Hoplodactylus delcourti* and Northland skink – *Oligosoma northlandi*; Hitchmough et al. 2016).

Declines in the abundance, distribution and diversity of reptiles in New Zealand have been primarily attributed to arrival of mammalian predators and habitat loss (Towns and Daugherty 1994). Following Polynesian arrival and the introduction of kiore, at least three reptile species (Tuatara, Dauvacel's gecko – *H. duvaucelii* and McGregor's skink – *O. macgregori*) are believed to have suffered local extinctions and range contractions, supported by fossil evidence and their currently disjunct distributions (Towns et al. 2001). A more recent example documents the devastating effect of Norway rats on a native tuatara population, causing rapid local extinction (more than 130 individuals lost within a year) following the rats introduction to Whenuakura Island in 1983-1984 (Newman 1986). Given predator impacts, a large proportion of New Zealand reptile species are heavily, or entirely, dependent on predator-free offshore islands or conservation reserves with predator-proof fences on the New Zealand mainland for their long-term survival (Towns et al. 2001).

In cases where reptiles can persist in the presence of predators, they remain suppressed at low population densities and with restricted local distributions, through mechanisms of both predation and competition. This is evident as densities of reptiles are generally much higher in environments which have either never had mammalian predators, compared to populations that co-exist with these predators, as well as through the growth of populations following predator removal (e.g. Towns 1991, Newman 1994, Lettink et al. 2010, Reardon et al. 2012, Norbury et al. 2013, Wilson et al. 2017). Lizards have also increased in abundance in landscapes where predators are regularly controlled but are not permanently excluded (Reardon et al. 2012, Wilson et al. 2017).

Clear evidence of strong top-down regulation by introduced rodents on lizards has come from Korapuki Island. Following rodent eradications, shore skink (*Oligosoma smithi*) capture rates increased by up to 3,600% over 9 years (Towns et al. 2001). This increase in the density of shore skinks was associated with shifts in their local distribution patterns, such that a much higher proportion of skinks now use patches of favourable habitat from which they were formerly excluded, through patch-specific increased predation risk (Towns 1996). A similar result has been shown for populations of Duvacel's geckos on Ōhīnau island. In the year following rat eradication, the capture rate increased by more than 420% and geckos spent

more time in formerly rat-dominated microhabitats (Hoare et al. 2007). Introduced mammals can negatively affect native lizards through competition as well as through predation. For instance, the known predators of reptiles – all introduced rodents, mustelids, feral cats and feral pigs (*Sus scrofa*), along with introduced rabbits (*Oryctolagus cuniculus*), also potentially compete with reptiles for food and shelter as they consume fruit, foliage and invertebrates (Blackwell 2005).

1.6 Indirect impacts of introduced mammals and habitat modifications

The direct impacts of introduced predators on native lizards, summarized above, are nearly always complicated or intensified by interactions and synergies between introduced predators, habitat modification, and introduced prey species (Norbury 2001, Towns et al. 2001, Norbury et al. 2013). Increases in fire frequency and intensity, land clearing, the introduction of grazing stock, replacement of native grasses with high-seeding pasture grasses, and pasture fertilization are common forms of habitat modification. These modifications can benefit introduced predators by providing them with additional resources, such as increasing the availability of seed for mice (*Mus musculus*) (Knox et al. 2012, Norbury et al. 2013). Simultaneously, these modifications reduce the food and refuge resources used by lizards through limiting the density and distribution of shrubby vegetation. Converting land to pasture and introducing stock also increases rabbit populations (Norbury et al. 2013, Whitehead et al. 2014). Rabbits and rodents can have indirect effects on lizard populations by enabling populations of feral cats, ferrets (*Mustela putorius furo*), stoats (*Mustela erminea*) and weasels (*Mustela nivalis*) – all generalist predators that consume lizards – to persist at higher population densities than would be possible in the absence of these introduced prey (Wilson and Lee 2010, Norbury et al. 2013). This indirect effect is a form of apparent competition termed 'hyperpredation' (Strauss 1991). Hyperpredation can explain the extinction of the Macquarie Island Parakeet (*Cyanoramphus novaezelandiae*) and the Macquarie Island Rail (*Rallus philippensis macquariensis*), following the introduction of rabbits and cats (Courchamp et al. 2000), as well as the looming probability of the island fox (*Urocyon littoralis*) extinction on the California Channel Islands following the introduction of pigs and subsequent colonisation by golden eagles (*Aquila chrysgetos*) (Roemer et al. 2002).

1.7 Study system: Central Otago drylands

Central Otago is a modified dryland ecosystem. New Zealand's drylands (or dry grasslands) are one of the most heavily modified and least conserved ecosystems in New Zealand (Rogers et al. 2005, Walker et al. 2005). While drylands constitute 19% of New Zealand's land area, 70% of native dryland habitat is thought to have been lost through land use-change since human settlement, and only 3% currently has legal protection (Norbury et al. 2011). Like other New Zealand habitats, the Central Otago drylands support a large and diverse introduced predator guild, with additional pressure from grazing stock and rabbits. However, this region also has a diverse assemblage of lizard species, and is the best example of high congeneric diversity remaining on the main islands (Towns and Daugherty 1994).

The drylands of Central Otago support at least 11 lizard species. This includes at least six skink species (*Oligosoma spp.*) and five gecko species, including the Jewelled Gecko (*Naultinus gemmeus*) and four species of taxonomically indeterminate 'Common Gecko' (*Woodworthia spp.*). However, while this diversity is currently rich, it is threatened. Of these 11 species, the NZTCS list two species as nationally endangered, the Grand skink (*O. grande*) and Otago skink (*O. otagense*), while a further two skink species (*O. inconspicuum* and *O. chloronoton*) and four species of gecko (*N. gemmeus, W. "Otago/Southland large", W. "Central Otago"* and *W. "Cromwell"*) are listed as 'at risk' (Hitchmough et al. 2016). This leaves just three species, two skinks (*O. maccanni* and *O. polychroma*) and one gecko (*W. "Southern Alps*") listed as 'non-threatened' in this landscape (Hitchmough et al. 2016). It has been suggested, however, that even populations of some of these 'non-threatened' species, while still widespread, may be seriously depleted (Norbury 2001).

Introduced predators in Central Otago include feral cats, ferrets, stoats, weasels, black rats (*Rattus rattus*), Norway rats, mice and hedgehogs (*Erinaceus europaeus*), in addition to introduced avian predators including Australian magpies (*Gymnorhina tibicen*), little owls (*Anthene nocturna)*, common starlings (*Sturnus vulgaris*) and self-introduced Australasian swamp harriers (*Circus approximans*). Investigations of predator diet from around New Zealand confirm that lizards are eaten by hedgehogs (Spitzen–van der Sluijs et al. 2009), stoats (Murphy et al. 2004), house mice (Towns and Elliott 1996, Lettink and Cree 2006, Norbury et al. 2014), weasels (Murphy et al. 2004), rats (Hoare et al. 2007), and introduced bird species

(Pierce and Maloney 1989). However, feral cats and ferrets are the dominant predators in dryland ecosystems (Reardon et al. 2012) and are the predators most often linked to lizard declines in these habitats (e.g. Middlemiss 1995, Norbury 2001). A simplified food web outlining the relationships between introduced and native species in New Zealand's drylands is presented in Fig. 1.

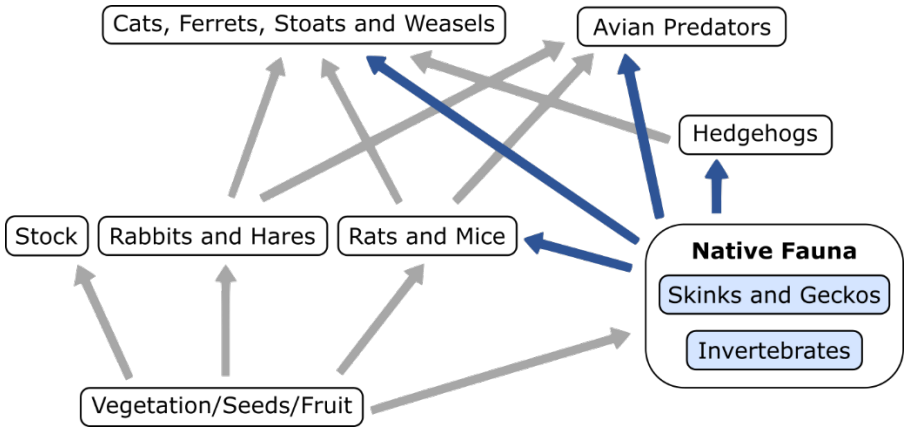

Fig. 1. Simplified food web for a typical New Zealand dryland ecosystem. Arrow direction represents the flow of energy between different trophic groups, with dark arrows indicating interactions between native fauna and predominantly introduced predators.

Central Otago's abundant rabbit population is the primary prey for both feral cats and ferrets in this system. Therefore, the population dynamics of these predator species are tightly linked to changes in rabbit availability (Norbury 2001). This means that rabbits can indirectly threaten secondary prey species, including native lizards, by maintaining populations of shared predators at higher densities than would otherwise be possible. Previous studies have shown that large rabbit reductions following baiting or the release of rabbit haemorrhagic disease virus (RHDV) have led to decreased sightings (Norbury and McGlinchy 1996, Norbury et al. 2002, Cruz et al. 2013), lowered survival (Norbury pers. comm.), and shifts in the behaviour (Norbury et al. 1998, Murphy et al. 2004) of feral cats and ferrets. While sustained reductions of rabbits are predicted to have positive effects in the long-term, the immediate effects of rabbit control can be negative for native lizards. This is because in an environment where rabbits have declined abruptly, the temporarily still abundant predators may increase their consumption of lizards as a form of secondary prey (Norbury 2001). Rabbits can also

negatively impact native lizards, as they are grazers, and contribute to habitat degradation. One study in the region found that four months of rabbit exclusion from areas of grassland increased pasture yields by 600% (Norbury and Norbury 1996). The effects on habitat quality of rabbit grazing are compounded by livestock grazing (Scroggie et al. 2013), as occurs regularly on the pastoral leases which make-up the majority of land tenements in dry grassland ecosystems. Grazing has direct impacts for lizards as it reduces lizard access to food and reduces the structural complexity of dryland vegetation, therefore reducing lizards' access to refuge. Reductions of structural complexity of vegetation have previously been linked to increased hunting success for predators (McGregor et al. 2015), and the decreased survival of prey species in predator rich environments (Norbury and van Overmeire 2019).

1.8 Conservation of dryland lizards

Managing the threat of predators, grazing and land-use change to promote the conservation of native dryland lizards is an ongoing challenge. The construction of multiple predator-proof enclosures in the areas surrounding Macraes Flat and Alexandra has been a critical step in seeking to secure nationally (and globally) endangered populations of Grand and Otago skinks. However, these populations not inside fences or subject to landscape-scale predator control have continued to decline (Reardon et al. 2012). The enclosures, along with some areas of long-term predator control, have also enabled researchers to investigate the effects of predator density on a wider range of co-occurring lizard species (Norbury et al. 2013, Wilson et al. 2017). Dryland lizard conservation is complicated by interactions among predators, prey and vegetation (Fig. 1), which mean that management actions can lead to potentially unexpected outcomes (Ramsey and Norbury 2009, Norbury et al. 2013, Pech and Maitland 2016). Understanding how species interact within a local ecosystem is an essential tool for environmental managers seeking to conserve native species. However, despite long-term programs of predator and rabbit control, there remain gaps in our understanding of the interactions at play in New Zealand's dryland ecosystems.

1.9 *Study aims*

The broad aim of this study is to gain a better understanding of the interactions between lizards and introduced predators in New Zealand's dryland environments. It is hoped that a

deeper understanding of these interactions will increase the capacity of managers to effectively conserve these native species.

The more specific aims of this study are two-fold:

1) To better understand the extent to which New Zealand lizards remain naïve towards the threat of introduced mammalian predators. I tested whether McCann's skinks *(O. maccanni*), an officially 'non-threatened' dryland lizard species, responded to predation cues associated with feral cats. By testing two different populations of McCann's skink, one from an area where mammalian predators are unmanaged, and one where mammals have been excluded via trapping and fencing, we also aimed to determine how predation pressure related to management practices might shape the response of McCann's skinks to predation risk.

2) To better understand the indirect effects of rabbits on lizards within dryland habitats. How does rabbit abundance relate to ferret density and ferret diet? Here, I aimed to understand the indirect impacts of rabbit control on populations of lizards (and invertebrates), and the extent to which rabbit control could be an effective management tool in the fight to conserve native prey species in the New Zealand drylands. To do this I utilised an existing dataset and re-analysed data on rabbit abundance, ferret density and ferret diet collected using recurrent surveys between 1994 and 1996 at three dryland sites.

Specific aims are developed in chapters 2 and 3 of this thesis. These chapters are presented as manuscripts that have been submitted for publication.

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CHAPTER 2

Rapid gain and loss of predator recognition by an evolutionarily naïve lizard

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The authors' contribution to this manuscript is as follows;

HC, MJ, CJ, RP an GN conceived the ideas and methodology; HC and BB collected study animals, conducted the experiments, and processed the images; HC analysed the data; HC led the writing of the manuscript. All authors contributed critically to the manuscript.

The undersigned agree with the above stated proportion of work undertaken for this manuscript that has been submitted as:

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ABSTRACT

The introduction of mammalian predators typically results in loss of native biodiversity due to naiveté of native prey to novel predators. In New Zealand, an island system with virtually no native mammalian predators, introduced mammalian predators threaten a large proportion of the native fauna. A critical step in adapting to introduced predators is the ability to recognise and respond to a novel predation threat. Whether New Zealand's lizards can do this has been little tested. We compared the basking behaviour of native McCann's skinks (*Oligosoma maccanni*) when exposed to a live cat (*Felis catus*), cat body odour, a model raptor (representing a coevolved predator), or procedural controls. We inferred predator recognition from reductions in individual basking frequency and higher selection for basking sites with greater refuge availability. We tested these behavioural responses for two skink populations: one from an area with high abundance of mammalian predators including feral cats, the other from a fenced conservation reserve where predators have been excluded for over 10 years. Skinks from the high-predator population reduced basking frequency when exposed to cat and raptor cues, whereas skinks from the low-predator population did not. These results suggest that within approximately 150 years of exposure to novel predators, McCann's skinks can recognise the threat posed by cats. However, they also demonstrate that predator recognition and antipredator behaviours are not necessarily retained once gained. The rapid loss of basking-related antipredator behaviours is likely to reflect the high fitness costs of reduced basking for this species. Our results indicate that the behavioural response of skinks is flexible, and that skinks maximise individual fitness by balancing the risk of predation with the costs of antipredator behaviours.

Keywords: anti-predator, conservation fencing, invasive predator, feral cat, New Zealand

INTRODUCTION

Introduced predators have disproportionate impacts on native prey (Salo et al. 2007) and are a major threat to biodiversity globally (Doherty et al. 2016). The impacts of introduced predators are especially clear for island systems, and are generally attributed to prey naiveté, whereby prey fail to mount effective antipredator responses (Cox and Lima 2006). However, prey naiveté is dynamic, and given sufficient experience of predators, prey populations can acquire responses that may allow them to coexist with once-novel predators (Carthey and Blumstein 2018). The first step in overcoming naiveté is recognising novel predators as a threat (level 1 naiveté sensu Banks and Dickman 2007), as this is necessary for prey to mount an effective response (Lima and Dill 1990). Predator recognition can be assessed through tests of cue discrimination – specifically the ability of prey to discriminate a predator cue from a non-predator cue.

A number of factors influence the likelihood that a particular prey species will recognise a novel predation threat, all of which depend on prey species' experience with predators over both evolutionary and ecological time scales (eco-evolutionary experience) (Carthey and Blumstein 2018). For example, the 'predator archetype hypothesis' predicts that experience with a morphologically or behaviourally similar predator (an 'archetype'), can prompt recognition of an introduced predator threat (Cox and Lima 2006). This mechanism can explain how an insular population of tammar wallabies (*Macropus eugenii)*, which had never encountered a fox (*Vulpes vulpes)*, initiated an antipredator response when confronted with a fox model for the first time, given their evolutionary experience with marsupial thylacines (*Thylacinus cynocephalus*) and recent exposure to cats and dogs (*Canis lupus*) (Blumstein et al. 2000). Absence of a suitable archetype can explain vulnerability of island species to introduced predators.

The length of time since introduction of a novel predator will also independently influence prey naiveté because predator recognition can develop via 'rapid change' mechanisms including plasticity, learning and rapid evolution (Carthey and Blumstein 2018). The rate at which antipredator behaviours develop depends on factors including the intensity of predation, the type of predator cue (e.g. visual/olfactory/auditory), the fitness costs associated with expression of antipredator traits, the heritability of specific antipredator traits and their genetic architecture, and the cognitive capacity of prey (Strauss et al. 2006, Sih et

al. 2010). This complexity limits current predictions on acquisition of predator recognition. Information on this is particularly relevant for threatened fauna, as it is only through understanding predator recognition capabilities, as well as the potential mechanisms involved, that we can obtain a conservation prognosis for species in the presence of current and future predator threats (Carthey and Blumstein 2018).

More than 80% of New Zealand's native lizard species listed under the New Zealand Threat Classification System (NZTCS) are currently classed as either 'threatened' or 'at risk' (Hitchmough et al. 2016), and a large proportion of New Zealand's lizards now survive only on mammal-free offshore islands, or inside mammal-free fenced reserves on the mainland (Towns et al. 2001). On human arrival, New Zealand's mammal fauna consisted of just three species of small insectivorous bats (King 1990), and while there is fossil evidence of other mammal species, including at least one mammal likely to have consumed small vertebrate prey, these species are likely to have been extinct for at least several million years (Worthy et al. 2006, Hand et al. 2018). Therefore, New Zealand lizards lacked experience with mammalian predators before several were introduced with two distinct waves of human colonisation (Polynesians c. 1280 AD and Europeans c. 1800 AD). Introduced lizard predators include cats (*Felis catus*), ferrets (*Mustela putorius furo*), stoats (*Mustela erminea*), weasels (*Mustela nivalis*), rats (*Rattus* sp.), mice (*Mus musculus*) and hedgehogs (*Erinaceus europaeus*) (King 1990, Blackwell 2005).

Because maximising basking opportunities has direct links to increased fitness in lizards (Downes 2001), there should be selection for New Zealand's lizards to assess the local predation risk associated with basking. This requires discrimination of predator cues to minimise predation by reducing basking frequency or by shifting basking to safer locations (e.g. closer to refugia) when predation risk is high. Assessing risk would also enable lizards to minimise sub-lethal effects of excessive wariness when risk is low.

Our aims are to establish whether New Zealand native lizards can recognise and respond to novel predator cues, and to assess the time-scales over which antipredator responses can change. We measured the basking behaviour of two populations of McCann's skink (*Oligosoma maccanni*) in response to different predation risk scenarios (treatments). Skink populations were sourced from an area of high mammalian predator density, and from within a conservation fence where mammalian predators have been absent for 3-4 skink generations

(Cree and Hare 2016). Treatments included the presentation of whole-body cues from a novel predator (a live feral cat), visual cues of a co-evolved predator (a model raptor), and a novel olfactory cue (cat scent). Both skink populations co-exist with native and introduced avian predators. McCann's skink is a relatively common and widespread species listed as 'non-threatened' under the NZTCS (Hitchmough et al. 2016), which has persisted in areas with large and diverse predator populations. It is therefore an ideal species to test whether any of New Zealand's lizards have moved beyond complete naiveté to mammalian predators.

We used this system to answer the following questions:

a) Can McCann's skinks discriminate cues of an introduced mammalian predator, the feral cat, from control cues?
b) Has the recent removal of introduced mammalian predators from a fenced reserve diminished the response of McCann's skinks to predation risk?
c) Do McCann's skinks balance the fitness benefits of predator avoidance against associated costs?

If skinks had developed the ability to discriminate novel predator cues, we predicted that in the presence of cat cues individual skinks would be observed basking less frequently and would preferentially bask in safer sites (closer to refuge). We also predicted that while both populations would demonstrate a similar antipredator response to a raptor cue (a coevolved and ubiquitous threat), the population currently without mammalian predators would have a weaker antipredator response to cat cues than the skinks from the high-predator population. Given that reducing basking has high fitness costs, and that at the time of testing these costs were expected to be particularly high for male skinks (basking is essential for spermatogenesis), we predicted that male skinks would bask more frequently than female skinks, and that skinks would target any reductions in basking to the riskiest periods of each treatment day.

METHODS

Study sites and lizards

Skinks were collected from two populations near Macraes Flat in eastern Otago, New Zealand. Skinks from the 'low-predator population' were sourced from a fenced reserve (45˚27'02"S,

170˚26’20”E, 575 m a.s.l.) which has been free of all mammalian predators (excluding occasional incursions of house mice) since August 2006 (Reardon et al. 2012). Skinks from the ‘high-predator population’ came from ‘Golden Point’, a 20 ha reserve (11 km north of the fenced population; 45˚20’58”S, 170˚25’30”E, 340 m a.s.l.) with no formal predator control (DOC personal communication, 2018) where skinks coexist with six potential predators - cats, ferrets, stoat, hedgehogs, Norway rats (*Rattus norvegicus*) and house mice – as confirmed by a camera survey conducted at the time of skink collection (99 trap nights). Introduced mammalian herbivores, including European rabbits (*Oryctolagus cuniculus*), red deer (*Cervus elaphus*), and feral pigs (omnivores; *Sus scrofa*) are also present in this area.

The vegetation of the region has been heavily modified by fire, land clearing and grazing, and is a mosaic of introduced pasture grasses (e.g. *Agrostis capillaris*), native tussock (*Chionochloa rigida*, *C. rubra*) and shrublands dominated by native manuka (*Leptospermum scoparium*) (Bibby 1997). The high-predator site had more rock cover (patches of scree) and tall introduced grasses, while the low-predator population had more native tussock, moss, and low manuka shrub cover (Appendix S1). Potential avian predators are ubiquitous across the region and include Australasian Harriers (*Circus approximans*; most frequently observed), New Zealand Falcons (*Falco novaeseelandiae*), and introduced Australian magpies (*Gymnorhina tibicen)*, common starlings (*Sturnus vulgaris*) and little owls (*Anthene nocturna*) (Marchant et al. 2006, Reardon et al. 2012).

We collected 32 adult skinks (16 males and 16 females) from each population in January 2018 using pitfall traps. Lizards were sexed using hemipene eversion and were deemed adult if hemipenes were readily everted (males) or if individuals exceeded a minimum snout-vent length (SVL) of 49 mm (females) (Cree and Hare 2016). All lizards were likely at least two years old, based on seasonal breeding and presence of several size classes. Captured skinks were transported to the laboratory for acclimation and behavioural testing and released at site of capture on completion of the study. Details on animal husbandry are in Appendix S2.

Experimental design and set-up

Behavioural trials were conducted over four consecutive weeks in January/February 2018. A different group (groups 1-4) was tested each week. Each group contained 16 lizards, with four males and four females from each population. Individuals of each sex were randomly

allocated to groups at the beginning of the experiment. Each week, each population was tested in one of two arenas, located in different rooms. The arena used for testing each population was alternated between weeks. Before testing, each lizard was uniquely marked using a xylene-free paint pen. We also recorded (a) snout-vent length (SVL), (b) if an individual had a tail-break (observable as an un-naturally short tail for skinks that had not regrown their tail to its pre-broken length, or as a change in patterning on the regrown tail), and (c) the vent to tail-break distance (a measure of tail-break severity).

Following a laboratory acclimation period of between five and 26 days, each group was acclimated in the testing arena for 3 days before the behavioural trials. They were then exposed to one of the four following treatments each day over successive days (Table 1; further details in Appendix S3): (a) procedural controls only, (b) a caged live female feral cat (Fig. 1a), (c) cat scent (collected via towelling which feral cats slept on for 7 days prior to use), and (d) a taxidermy harrier in flight (Fig. 1b).

Table 1. Procedures followed for predator exposures on each of the four treatment days (each day is represented by a separate column). Treatment exposures that differ to the procedural control are indicated in *italics.*

Daily Exposures	*Ctrl*	*Cat*	*Cat scent*	*Raptor*
Tile towelling (422 min)	no scent	no scent	*½ with cat scent*	no scent
AM Exposure 1 (32 min)	cage	cage *+ cat*	cage	cage
AM Exposure 2 (26 min)	pulley	pulley	pulley	pulley *+ raptor*
PM Exposure 1 (26 min)	pulley	pulley	pulley	pulley *+ raptor*
PM Exposure 2 (32 min)	cage	cage *+ cat*	cage	cage

Behavioural trials were conducted within 3.66 m diameter, 12-sided plastic-walled arenas with a 5 cm layer of sand/gravel substrate (Fig. 1c). Each arena had eight basking sites consisting of terracotta tiles (W19.5 cm x L19.5 cm x H1.5 cm) positioned 15 cm beneath a 42W (610 lumen) halogen lamp. Basking sites were arranged symmetrically in two parallel rows. On the 'high-refuge' side of the arena, refuges were added in close proximity (20 – 30 cm) to each basking site in one row. On the other 'low-refuge' side, the basking sites were more distant from refuge (1.2 m). Refuge consisted of tussocks (*Carex testacea*, similar in size and structure to tussocks at the field sites) and upturned terracotta saucers (13 cm diameter with a 2x2 cm access hole on the side, structurally equivalent to rock crevices at the field sites). During the live cat or cage exposures the cat cage was placed in the centre of the arena (Fig.

1c). The cat-scented towels or unscented control towels were placed over part of each basking tile. Exposure of lizards to cat-scented towelling was associated with two neighbouring high-refuge basking sites and two neighbouring low-refuge basking sites located in opposing corners of the arena. During the raptor exposure the model was 'flown' on a string through the centre of the arena between the rows of high-refuge and low-refuge basking sites.

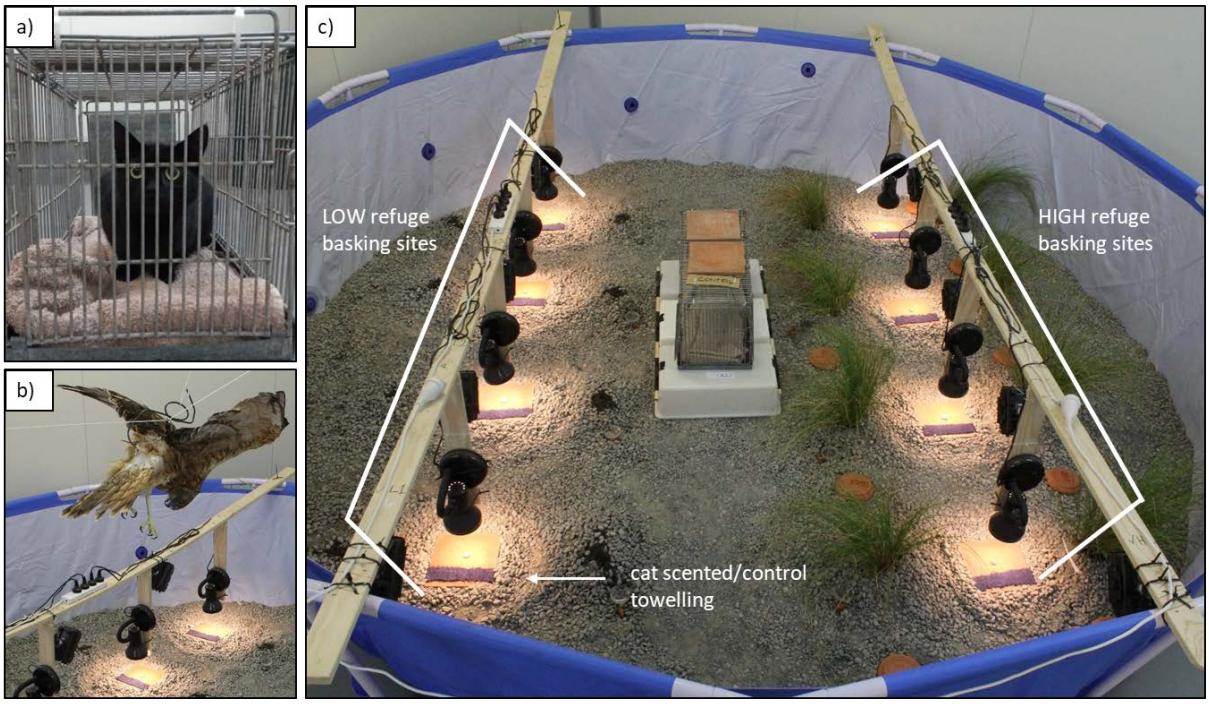

Fig. 1. Trial set-up: a) a caged cat for the live cat exposure treatment; b) the taxidermy raptor attached to the pulley system; c) rows of four 'low refuge' and four 'high refuge' basking sites. Each basking site was associated with towelling for the scent trials and, when in use, the cage was placed in the centre of the arena.

Each basking tile had a camera (Bushnell HD Aggressor) positioned overhead, programmed to capture time-stamped images of the tile once every minute from 0900-1600 hours. 'Thermachron' ibutton loggers were placed in the centre of each tile, directly below the heat source, and one near each arena wall, and programmed to record the temperature once every hour for 24 hours a day for the duration of the experiment. Ninety-five per cent of the 0930-1530 basking site readings fell between 24 and 33˚C, while the minimum ambient temperature recorded was 19˚C. These temperatures are within the natural range experienced by this species at the field site, where the lizards are active between 16˚C and 33˚C (Holmes and Cree 2006).

Image processing and data analysis

The identity of all basking skinks, based on their painted markings (Appendix S4), was recorded in the metadata of all photos in the period 0900-1600 each day via image tagging in ExifPro v2.1 (http://www.exifpro.com). An individual was considered basking when any part of its body crossed the basking tile in a photo. Records were excluded from analysis if less than half of the skink was visible because the skink was between the tile and the towelling (970 or 2.87% of records excluded) or if it could not be identified definitively (e.g. skinks lying across each other; 280 or 0.83% records).

We used generalized linear mixed models and multimodel inference to analyse the effect of population (low or high predator), treatment (control, cat, cat scent or raptor), sex (male or female) and tile temperature (continuous between 27˚C and 33˚C +/- 1˚C) on three response variables, expressed as proportions of records in each category: 1) basking frequency, 2) preference for basking sites based on refuge availability, and 3) preference for basking sites with or without cat scent on cat scent treatment days. We modelled the first and second response variables separately for three time periods; (a) all day or 422 min/day, (b) during the 62 min/day cat exposure period, and (c) during the 52 min/day raptor exposure period, to test for evidence of a long-lasting temporal and spatial avoidance of predator threats (all-day avoidance), or whether avoidance was temporally targeted to periods of peak threat (avoidance limited to the cat and raptor exposure periods). We also modelled selection for basking sites treated with cat scent *versus* non-scented basking sites across all treatment days to separate preference for certain tiles from response to cat scent, which was present only on the cat-scent treatment day. Because previous studies have found links between behaviour and size or tail-loss characteristics (Bateman and Fleming 2009), we tested for differences in SVL and tail-loss between populations (Welch's t-test) before modelling and used linear models to investigate if these covariates affected basking frequency.

For all analyses, we initially ran 15 candidate models (Appendix S5). All candidate models, including the null model, incorporated fixed effects for testing arena (two arenas), daily mean maximum temperature in each arena (continuous between 27.0 and 33.3 ˚C), and testing day for any given testing week (days 1 - 4). Random effects included testing group (eight groups of eight lizards), individual (N = 64), and an observation level random effect to account for data over dispersion (N= 255). Candidate models subsequent to the null model incorporated

increasingly complex combinations of population (*'P'*, levels: low predator, high predator), treatment (*'Tr'*, levels: control, cat, cat scent and raptor) and sex (*'S'*, levels: M, F) fixed effects, as well as biologically meaningful interactions between these terms (Appendix S5).

To analyse basking behaviour over the entire treatment day (*all day period*), or just the *cat exposure period* or the *raptor exposure period*, we used the same methods on subsets of the data. A number of models failed to converge for the cat and raptor exposure periods, which we solved by running simpler models that lacked a temperature interaction term. This was justified by the lack of evidence for an effect of arena, temperature or testing day on basking site preference for the *all day period*. Because some individuals were rarely observed basking, before modelling basking site preferences for high vs. low refuge sites we removed observations for skinks when they were observed basking on less than 50 occasions (bottom quartile; *all day* models) or 10 occasions (*cat* and *raptor exposure period* models).

Models were run using the *glmer* function from the *lme4* software package in R (Bates et al. 2014a, R Core Team 2017). Because all response variables were proportions, models used a binomial distribution with a logit link. All models used the 'bobqa' optimiser from the R package *minqa* (Bates et al. 2014b) with the maximum number of evaluations set to 100,000 to assist with model convergence. Given our sample size and the number of model parameters, we ranked all candidate models for each analysis using ΔAICc for small sample size (Burnham and Anderson 2002) and considered models to form part of a best model set if they had both a ΔAICc less than six and had no simpler nested models with a lower ΔAICc (Richards 2008). We used the *MuMIn* package (Barton 2013) for model selection and to quantify marginal (R^2m) and conditional R^2 (R^2c) values, where R^2m quantifies the variance explained by fixed effects alone, and R^2c quantifies the variance explained by the entire model (incorporating both fixed and random effects) (Nakagawa et al. 2013). For any response variable where the fixed effects in the top model explained considerable variance (at least 18% of data variance - only the skink basking frequency models), we passed the top model (lowest AICc) to the *emmeans* package (Lenth 2018). This package calculated the marginal means (least-square means) for basking frequency with each predator cue treatment within each population. It also provided a graphical output of comparisons between treatments, odds ratios and adjusted p-values (Tukey multiplicity adjustment).

RESULTS

Skinks were recorded basking 19.4% of the time (32,518 out of 167,610 images), for a mean of 128 minutes/day (range 0-349 min). After removing records on days when basking was observed on less than 50 occasions, on average skinks basked at high-refuge sites 80% of the time (n=190, range = 36-100%). There was some evidence of behavioural consistency across treatment days, such that regardless of treatment some individuals consistently basked frequently (e.g. 4th quartile) and others only occasionally (e.g. 1st quartile). The number of individuals that consistently basked above the 128 minutes/day average was skewed towards the low-predator population (15 of 19 individuals) and towards males (14 of 19 individuals).

In addition to testing the effects on basking behaviour of population, sex and predator cue treatment, we also analysed the influence of temperature, lizard size and tail breaks. The temperature of basking sites varied both between arenas and across testing days (Appendix S6). Skinks from both populations increased basking frequency at higher temperatures. However, this relationship was much stronger among lizards from the high-predator population (Linear regression; $F_{(126,127)} = 60.275$, $p < 0.001$, $R^2 = 0.32$) than from the low-predator population ($F_{(125, 126)} = 8.02$, $p = 0.005$, $R^2 = 0.06$) (Appendix S7). Lizard size (SVL) did not vary between the high-predator (mean ± SD = 59.7mm ± 3.5mm) and low-predator (58.2mm ± 4.1mm) populations ($t_{(60.82)} = 1.42$, $p = 0.16$). There was no relationship between SVL and individual basking frequency ($F_{(62,63)} = 2.94$, $p = 0.09$, $R^2 = 0.05$; Appendix S8), or SVL and preference for high or low refuge basking sites (Linear regression; $F_{(53,54)} = 1.72$, $p = 0.03$). Tail breaks were discernible in 85% (54 of 64) of skinks and was equivalent between sexes (84% both sexes) and populations (88% and 81% in the low- and high-predator populations respectively). However, tail-loss severity (measured as the vent to tail-break distance – the shorter this distance, the greater the severity) was significantly higher in the low-predator population (30.0mm ± 17.1mm) compared to the high-predator population (56.0mm ± 17.7mm) ($t_{(51.91)} = 5.51$, $p < 0.001$). Individuals with more extreme tail loss basked more frequently ($F_{(52,53)} = 4.69$, $p = 0.04$, $R^2 = 0.08$; Appendix S9). However, as individuals with more extreme tail loss were also disproportionately associated with the low-predator population, it was not possible to isolate the effect of tail loss extent from the broader effect of population. There was no relationship between severity of tail-loss and basking site preference ($F_{(44,45)} = 0.94$, $p = 0.33$).

Basking frequency

Population, sex and predator cue treatments were all important predictors of skink basking frequency and were included in the best-supported models for all testing periods, with these models carrying much of the AICc weight (Appendix S10). Population and sex had a relatively large effect on basking frequency that was consistent across all treatments and all periods. Male skinks consistently basked more frequently than females (Fig. 2; mean difference 62 min/day) and skinks sourced from the low-predator population basked more frequently than skinks from the high predator population (Fig. 3; mean difference 68 min/day). In the best-supported model for each period (*all day*, *raptor exposure*, *cat exposure*), the fixed effects explained between 18 and 37% of data variability (Appendix S10).

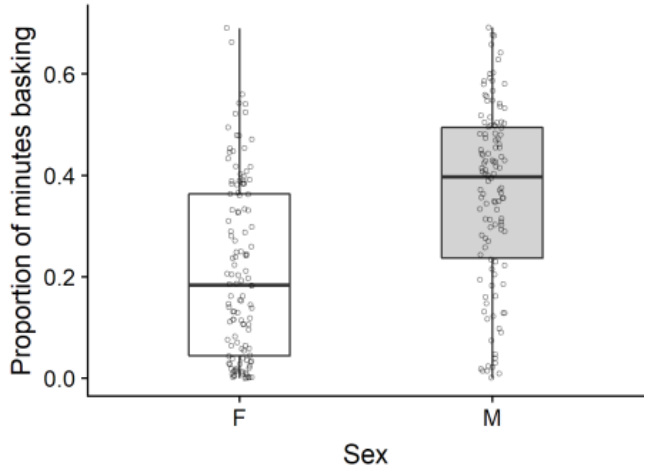

Fig. 2. Proportion of minutes individual male (M) and female (F) skinks were observed basking (includes data for all skinks for each treatment day, n=255). Boxes show the median and interquartile range of the data; whiskers represent 1.5 times the interquartile range, or the range of the data, whichever is smaller.

Skinks altered their basking frequency in response to predator cues and this response differed with source population (Fig. 3). A population:treatment interaction was included in the most parsimonious models for both the *cat exposure period* and *raptor exposure period*, but not the *all day period* (Appendix S10). During the *cat exposure period,* skinks from the high predator population reduced basking in the presence of a live cat (2.76 times less likely to bask) and cat scent (2.29 times less likely to bask) relative to the procedural control, but skinks

from the low predator population did not (Fig. 3, Appendix S11). Similarly, during the *raptor exposure period* only the high predator population reduced basking when exposed to a raptor cue (8.40 times less likely to bask) and cat scent (3.65 times less likely to bask) (Fig. 3, Appendix S11).

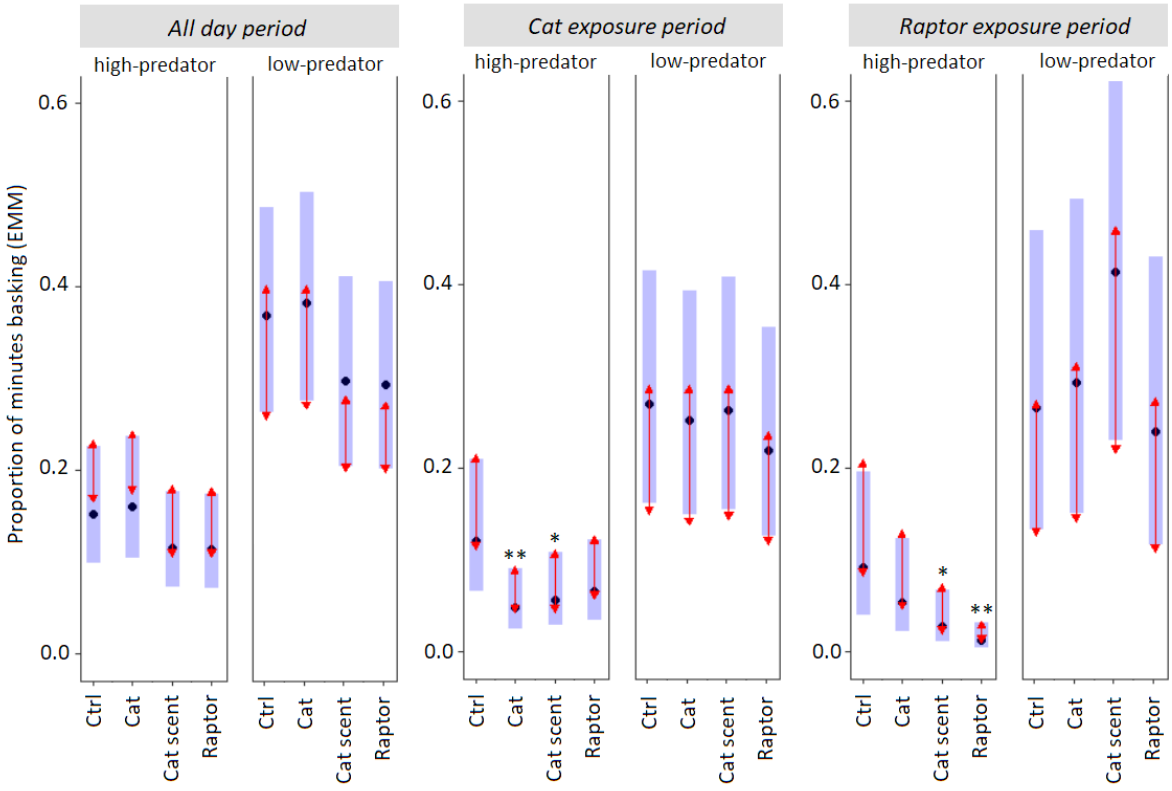

Fig. 3. Proportion of minutes skinks were estimated to bask during three periods: *all day period* (422 min/day), *cat exposure period* (62 min/day) and *raptor exposure period* (52 min/day). Points represent the estimated marginal means (EMM) and 95% confidence intervals (filled bars) for each population/treatment combination based on the best ranked model for each period (Table 3). Non-overlapping arrows indicate significant differences between groups within each model (adjusted $p < 0.05$, Tukeys HSD test). Within each population, responses to predator treatments that differ significantly from the control are indicated with asteriks (* $p < 0.05$, ** $p < 0.001$).

Basking-site preference

Population, treatment, sex and temperature were all relatively poor predictors of basking-site preference, with any combination of these predictors explaining a maximum of 4% of the data

variability (Appendix S12). Source population was included in the best-supported model for basking site preference over the *all-day period* and for the *raptor exposure period*, although inference was weak given low explanatory power of these models. On average, all skinks preferred high-refuge over low-refuge basking sites, more so for skinks from the high-predator population during both exposure periods (Appendix S12). The best-supported model for basking site preference during the *cat exposure period* included only a treatment effect (Appendix S12). Both populations were more likely to bask at sites with high refuge availability while a live cat was in the testing arena (cat treatment during *cat exposure period*) compared to during the same period on days with only procedural controls. There was no evidence that skinks avoided cat-scented tiles, with the null model included in the candidate model set (ΔAICc = 0.50), at most 1% of data variability explained by this variable, and a relatively small effect size (0.38 ±0.17) (Appendix S12).

DISCUSSION

Can McCann's skinks discriminate cues of the introduced feral cat from control cues?

Exposing skinks from the high-predator population to both the whole-body cues of a live cat, and cat scent alone, resulted in temporary reductions in basking frequency, suggesting that for at least one species of New Zealand lizard, the period of exposure to a novel predator has been sufficient for the development of cue discrimination and an adaptive behavioural response. Feral cats are unlikely to have become established in Central Otago before the establishment of rabbits, approximately 150 years ago (King 1990); therefore, these adaptations have developed within a maximum of 50 skink generations (Cree and Hare 2016). Rapid development of antipredator behaviours to novel predator cues have been reported across a range of taxa, both within New Zealand and globally. Very rapid response times include that of Ibiza wall lizards (*Podarcis pityusensis*) to the chemical cues of a snake within a decade of their introduction (Ortega et al. 2017) and evolution of innate predator recognition of an introduced red swamp crayfish (*Procambarus clarkii*) by tadpoles (*Pelophylax perezi*) within 20 years (Nunes et al. 2014). Examples from Australasia, include nest-defence by New Zealand robins (*Petroica australis*) when confronted with cues of a stoat (within c. 100 years of exposure; Maloney and McLean 1995), and the response of two

Australian lizards (*Morethia boulengeri*, *Christinus mamoratus*) to cat and fox scent cues (within 150 years of exposure; Webster et al. 2018).

Two previous studies found little evidence that New Zealand lizards from mammal-invaded areas (including *O.polychroma, O. zealandicum* and *Woodworthia maculata*) responded to the chemical cues of either ship rat (*Rattus rattus*) or hedgehog urine or faeces (Dumont 2015, Monks et al. 2019). Similarly, while a skink (*Caledoniscincus austrocaledonicus*) from New Caledonia (a nearby island with similar evolutionary history) avoids the chemical cues of recently introduced ship rats and cats, a native gecko (*Bavayia septuiclavis*) does not (Gerard et al. 2014). Possibly, these studies failed to detect an antipredator response because of the cue type presented (Carthey and Banks 2014). We found stronger evidence of an antipredator response when visual cues of predators – a live cat and a model raptor – were presented than when lizards were exposed to chemical cues alone (although a direct comparison is difficult due to differences in the duration of exposure to each cue type). This supports previous suggestions that New Zealand lizards may rely heavily on non-chemical cues (e.g. visual, auditory) to detect and respond to predators (Monks et al. 2019). Because visual cues provide greater certainty of imminent predation risk, prey often respond more strongly to visual cues of a predator than to chemical cues (Carthey and Banks 2014). However, the response of New Zealand prey to visual cues may be further amplified if visual cues have been an important means of detecting predators historically (Carthey and Banks 2014), as seems likely given the primarily visual hunting mode of New Zealand's native predators (Meyer-Rochow and Teh 1991, Worthy and Holdaway 2002).

Has the recent removal of introduced mammalian predators from a fenced reserve diminished skinks response to predation risk?

While the high-predator population temporarily reduced basking frequency in the presence of a live cat, cat scent and a model raptor, the low-predator population did not reduce basking in the presence of any of these potential threats. This suggests that removal of mammalian predators has led to the loss of cat recognition within 3-4 skink generations. Loss of predator recognition and antipredator behaviour following release from predation pressure is a well-documented phenomenon within reptiles (Li et al. 2014, Brock et al. 2015) as well as other taxa (e.g. mammals - Blumstein 2002, fish - Kelley and Magurran 2003, birds - Beauchamp

2004), and it can often occur very rapidly (Jolly et al. 2018, Lapiedra et al. 2018, Muralidhar et al. 2019). This is because in lower-risk environments excessive predator avoidance can have strong fitness costs, and so selection can work to limit the retention of these behaviours (Smith and Blumstein 2008).

The recent removal of mammal predators appears to have diminished not only the response by skinks to the risk posed by cats, but also to avian predators. This was an unexpected result, given that skinks from the low-predator population coevolved with avian predators and continue to live in an area accessible to avian predators. A similar result has been recorded in a fish population, where it was concluded that isolation from one predatory threat (other predatory fish) diminished the antipredator response of prey fish towards a secondary predatory threat (predatory birds), even though exposure to this secondary predator threat continued (Wund et al. 2015). Additionally, a study on Agean wall lizards (*Podarcis erhardii*) has highlighted the importance of high predator diversity in determining the retention rates of particular antipredator traits (Brock et al. 2015). These results suggest that the retention of antipredator behaviours is complex and often difficult to anticipate.

Do McCann's skinks balance the fitness benefits of predator avoidance against associated costs?

Basking is tightly coupled with variation in fitness for lizards (Downes 2001), particularly for viviparous species in colder climates (Wapstra et al. 2010). To maximise fitness, individual lizards need to balance avoiding predation with performing behaviours that maintain metabolism, such as basking. This balance will change with predation risk. In the low-predator population, the high cost of reducing basking for this temperate, viviparous species may have favoured individuals that bask more frequently regardless of predator cues. As basking behaviour is closely associated with fitness, it should be particularly sensitive to changes in predation pressure. This means that reductions in basking frequency may have been lost particularly rapidly, while other antipredator behaviours may not have changed at this same rate (Blumstein 2002).

Timing of predator avoidance behaviours indicates flexibility in the response of McCann's skinks to spatial and temporal variation in predation risk that is based on balancing risk and costs. By temporally targeting costly antipredator behaviours, skinks can limit the sub-lethal

impacts associated with being overly wary during less risky periods. First, the high-predator population increased predator avoidance behaviours during periods of peak risk (*cat* and *raptor exposure periods*) but not over longer time periods (*all day period*). Second, male skinks consistently basked more frequently than female skinks, regardless of population or treatment. Our study took place after females had given birth, but during male spermatogenesis (Cree and Hare 2016) when basking is a key requirement (Saint Girons 1985). We would predict this sex-related pattern to change with time of year and reproductive phase (e.g. female skinks should bask more frequently than males in spring or early summer while pregnant), which could be readily tested.

Conclusions and recommendations for future research

Feral cats pose an enormous threat to native prey species globally (Medina et al. 2011). In our study region, native lizards including McCann's skinks, have been found in over 60% of feral cat scats, with several scats containing more than 30 individual lizards (n=124, GN unpublished data; Norbury 2001). Therefore, populations of even this common lizard species remain vulnerable to cats, despite our encouraging results that some New Zealand lizard species can reduce their evolutionary naiveté towards mammalian predators. The rapid loss of recognition of both novel and coevolved predators in skinks from a population not exposed to mammalian predators indicates that predator removal can increase prey naiveté and leave prey populations vulnerable once again to future increases in predation pressure. This means that the consequences of predator incursions could be particularly damaging for low-predator populations, highlighting the ongoing need for vigilant quarantine practices and fence maintenance (Muralidhar et al. 2019). Furthermore, the recent predator experience of source populations for reintroductions into areas of higher predation pressure needs to be carefully considered (Blumstein 2002).

How quickly and effectively prey populations are able to respond to changes in predation pressure depends on both the mechanisms underpinning the gain and loss of antipredator behaviours, and the efficacy of antipredator responses (Carthey and Blumstein 2018). Key priorities for future research are distinguishing amongst mechanisms and testing whether targeted management actions (e.g. increasing refuge availability) could improve response efficacy. Potential mechanisms currently include: (i) *labelling* whereby a prey species uses the

generalised features of a known predatory threat and applying it to novel threats, (ii) *rapid evolution* whereby selective predation alters the frequency of prey population genotypes, or (iii) *learning* whereby individuals develop behavioural responses following encounters with predators within their lifetime. The likely contribution of these mechanisms could be determined using appropriate control treatments to test for labelling, comparing cue discrimination of captive-bred offspring against their wild-caught parents to test for evidence of rapid evolution (e.g. Wund et al. 2015, Jolly et al. 2018), and comparing the response of individuals to predator cues over multiple exposures to test for learning (e.g. Maloney and McLean 1995, Li et al. 2014, West et al. 2018).

Particular challenges are to increase the range of native species tested for acquisition of antipredator responses to introduced predators, including loss of evolutionary naiveté, and to expand the range of cues tested. On the first point, relatively few species within the faunas of land masses where introduced predators are a major conservation threat, have been tested for the gain of appropriate antipredator responses. In New Zealand, this research has primarily focussed on the antipredator response of a number of bird species, with a more limited focus on the response of species from other taxa. Our study has shown that one common species of skink in New Zealand can recognise cues of an introduced predator. It is important to find out whether this ability is widespread amongst New Zealand's herpetofauna, given the high proportion that is threatened. McCann's skink may not be representative of the scale of the problem as it is is unusually resilient to introduced predator threats in the New Zealand context (populations remain widespread and abundant, they have been known to replace other native skinks in certain habitats, and they are listed in the non-threatened minority of New Zealand herpetofauna (Hitchmough et al. 2016)). On the second point, a range of cues need to be tested for response to introduced predators. This is particularly the case for research on antipredator responses in reptiles globally. Surprisingly few studies have tested the response of reptiles to non-human visual cues of predation risk (but see Stapley 2004, Li et al. 2014), despite evidence that reptiles often use visual cues to assess and respond to their immediate environment (e.g. Ammanna et al. 2014). In the New Zealand context, it would be useful to build on these experiments by repeating trials with visual as well as olfactory cues of other introduced predators (e.g. rats, hedgehogs, mustelids) to determine

the extent to which skinks can generalise risk avoidance behaviour across the introduced predator guild.

Differences in predator recognition abilities between species may provide a mechanistic hypothesis for patterns of species persistence and vulnerability. By conducting similar studies on a wider range of species differing in their susceptibility to predation, we may be able to determine the extent to which cue recognition contributes to the resilience of prey species in invaded systems. This research would greatly benefit from a consistent experimental design across studies and species, a process which would provide data suitable for robust cross-species comparisons.

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CHAPTER 3

Problems with prey-switching: short-term suppression of invasive primary prey increases predation on native prey

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Statement of Co-Authorship

The authors' contribution to this manuscript is as follows;

GN conceived the original experiment; RH and GN conducted the field work; RH processed ferret scats and recorded dietary intake; HC analysed the data and led the writing of the manuscript. MJ, CN, RP and GN contributed critically to the manuscript.

The undersigned agree with the above stated proportion of work undertaken for this manuscript that has been submitted as:

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ABSTRACT

The control of invasive species can have cascading and at times undesirable effects on the wider ecological community. Effective management requires that the ecosystem-wide effects of removing invasive species be understood. We investigated the effects of large-scale rabbit control on the abundance (numerical response) and diet (functional response) of an invasive predator (ferret, *Mustela putorius furo*) that preys on rabbits (*Oryctolagus cuniculus*), as well as the subsequent predation pressure experienced by alternative prey species (total response), in New Zealand's dryland habitats. Following rabbit control, ferret densities declined but surviving ferrets increased their per capita consumption of lizards and invertebrates, two key native prey groups. Rabbit control increased predation pressure for lizards, but decreased predation pressure for invertebrates. While rabbit control can negatively impact some groups of alternative prey up to 18 months post-control, it probably benefits them in the longer term because prey-switching by ferrets tended to reduce with time, and regeneration of vegetation previously over-grazed by rabbits is likely to reduce exposure of native prey to predation. While confirming these benefits will require longer-term monitoring, our results support management actions that limit short-term fluctuations in rabbit abundance and maintain them at low abundance.

Keywords: hyperpredation, apparent competition, numerical/functional response, rabbit control, ferret diet, lizard conservation

INTRODUCTION

A key challenge in biodiversity conservation is designing effective strategies to reduce the impacts of invasive species (Simberloff 2000, Clavero and Garcia-Berthou 2005). Most invaded ecosystems host multiple invaders, leading to a myriad of complex interactions among suites of invasive and native species. These interactions mean that while targeting invasive species for control or eradication can result in recovery of native species (e.g. Bellingham et al. 2010, Pedler et al. 2016), such positive outcomes are far from guaranteed (Pech and Maitland 2016). The more highly invaded the ecosystem, the more likely it is that control or eradication operations will have unexpected or undesirable consequences (Zavaleta et al. 2001).

Part of the problem is that invasive predators are often co-introduced with invasive prey, such as rabbits and rodents, which have high intrinsic rates of increase (Sinclair 1997). This can lead to hyperpredation (Smith and Quin 1996), a mechanism of apparent competition whereby invasive prey support high densities of an invasive predator which increases 'spill-over' predation onto native prey, which often have much lower intrinsic rates of increase (e.g. Sinclair 1997, Kelly and Sullivan 2010). The combined effects of hyperpredation and direct effects of habitat degradation and resource competition through over-grazing by invasive herbivores can be disastrous. For example, hyperpredation is the proposed mechanism of extinction of two endemic bird species on Macquarie Island. Here, invasive European rabbits (*Oryctolagus cuniculus*, hereafter 'rabbits') enabled invasive cats (*Felis catus*) to reach high population densities, which in turn led to unsustainable predation on the Macquarie Island parakeet (*Cyanoramphus novaezelandiae*) and the Macquarie Island rail (*Rallus philippensis macquariensis*) (Taylor 1979, Garnett and Crowley 2000). Apparent competition or hyperpredation is increasingly being identified as a threat and has been linked to declines in native prey across a wide range of taxa (reviewed in DeCesare et al. 2009).

Removing invasive prey can potentially reduce the impacts of hyperpredation and help protect native prey (Courchamp et al. 1999, Cruz et al. 2013, Norbury 2017). There is a risk, however, that prey-switching by invasive predators will lead to increased predation pressure on alternative native prey species as the primary invasive prey declines, particularly in the short term (Moleon et al. 2008, Wittmer et al. 2013a, Lurgi et al. 2018). Whether this happens

hinges on the *total response* of predators to changes in prey availability (Pech et al. 1992). The *total response* is the product of both the *numerical response*, which describes how predator abundance changes in response to changing prey availability (Solomon 1949), and the *functional response*, which describes how predators' per capita intake of different prey items changes in response to changes in prey availability (Holling 1959). The shape of the numerical response will determine the extent to which alternative prey species benefit from the control of primary prey species through reduced abundance of predators. The shape of the functional response determines the extent to which alternative prey will be harmed by these control actions as predators switch from a formerly abundant primary prey to alternative prey species. The total response describes the extent to which the benefits of the numerical response outweigh the impacts of the functional response, or vice versa, enabling an assessment as to whether control actions provide a net benefit for alternative prey.

In New Zealand, native biodiversity is threatened by both invasive generalist predators and invasive prey. Introductions within the last 200 years have led to abundant populations of cats, ferrets (*Mustela putorius furo*) and stoats (*Mustela erminea*), as well as extreme infestations of rabbits, which represent not only an ecological threat, but an economic threat to agriculture. Where these predators and rabbits co-occur, rabbits are typically the primary prey while alternative prey species are consumed opportunistically (Murphy et al. 2004). The impacts of these predators on alternative, predominantly native, prey species is particularly concerning for two reasons. First, coevolutionary isolation can lead to the naivety of prey towards novel eutherian predators (Banks and Dickman 2007). Second, because of lower reproductive rates, which are especially prevalent in New Zealand endemic species (Kelly and Sullivan 2010, Cree and Hare 2016), many endemic native prey cannot sustain the high predation pressure imposed by invasive predators. In heavily infested regions, rabbits are routinely culled using a variety of methods including shooting, baiting and the release of targeted viral agents such as rabbit haemorrhagic disease virus (hereafter RHDV). Despite this, the flow-on effects of rabbit control are not always well understood.

Ferrets and rabbits are key threats in New Zealand's dry shrub/grassland ecosystems (hereafter 'drylands') for numerous species of endemic and threatened lizards, invertebrates and birds, through both direct and indirect mechanisms (Norbury 2001). In spring 1994, a large-scale rabbit control program was implemented at two sites in New Zealand's drylands.

To assess the impacts of this management action, the two treatment sites as well as a third non-treatment site were monitored to record changes in rabbit abundance, ferret density, and the type and number of different prey species eaten by ferrets. Equivalent data sets that use a before-after-control-impact (BACI) experimental design are relatively scarce in management of invasive species (Courchamp et al. 2003a) and so these data provide an important opportunity to describe the numerical, functional and total response of a generalist predator to reductions in primary prey.

Based on prior knowledge of this and related systems we make the following predictions:

Numerical response. Given that rabbits are consistently the major prey item in ferret diet in studies conducted across New Zealand (Robertson 1976, Pierce 1987, Smith et al. 1995, Ragg 1998, Murphy et al. 2004) and elsewhere (Bodey et al. 2010), we expect both a reduction in ferret abundance and a reduction in the population growth rate of ferrets in response to rabbit reduction.

Functional response. Based on previous descriptions (Norbury 2001), and because ferrets are opportunistic generalists (Smith et al. 1995), we expect that ferrets will switch to alternative prey in response to declines in rabbit abundance.

Total response. We expect lags in the system to create a transition period, during which ferrets remain abundant but rabbits are scarce. We therefore expect the net effect of rabbit control on alternative prey to be negative in the short term, because of prey-switching by ferrets, but become increasingly positive with time post-control as densities of ferrets decline.

METHODS

Study sites

The study was conducted at three sites in modified, short-tussock dryland between February 1994 and March 1996. Two of the sites (Grays Hills and Bendigo) were treatment sites where rabbits were poisoned in September 1994, while one site (Earnscleugh) was not poisoned, providing a non-treatment site. All sites were monitored for 6 months before poisoning, and 19 months post-poisoning. The Grays Hills site (6000 ha) was located on Grays Hills station, 20 km east of Twizel in the Mackenzie Basin District (44˚ 17’ S, 170˚ 23’E). The Bendigo (2500 ha; 45˚ 2’ S, 169˚ 18’ E) and Earnscleugh (1000 ha; 45˚ 10’ S, 169˚, 17’ E) sites were located on

namesake stations in Central Otago, approximately 125 km to the southwest of Grays Hills. A large hydro-electric dam, which predators were unable to cross, separated the Earnscleugh and Bendigo sites by 24 km. All sites were on hill country with numerous rock outcrops at an altitude of 220-940m above sea level. The long-term average rainfall for the three sites ranged from 385-456 mm/year and mean monthly air temperatures range from 3˚C in July to 17˚C in January. In late June 1995 the region experienced unusually heavy snowfalls, with snow persisting for 2-3 months.

All sites were on pastoral properties with extensive sheep grazing. Prey species other than rabbits, both native and invasive, were present at all sites. Native vertebrate prey included at least one species of bird (pipit, *Anthus novaeseelandiae*), several species of lizard, including common skinks (*Oligosoma polychroma*), McCann's skinks (*O. maccanni*), and several gecko species (some yet to be formally described, *Woodworthia* aff. *maculatus*). Native invertebrates included grasshoppers, weta, beetles, beetle larvae, flies, bees, cicadas, earwigs and spiders. Introduced avian prey species included skylarks (*Alauda arvensis*), yellow hammers (*Emberiza citrinella*), chaffinches (*Fringilla coelebs*), thrushes (*Tardus philomelos*), blackbirds (*Tardus merula*) and California quail (*Callipepla californica*). Invasive mammalian prey included hedgehogs (*Erinaceus europaeus*), mice (*Mus musculus*), rats (*Rattus norvegicus*), possums (*Trichosurus vulpecula*) and hares (*Lepus europaeus*). Other predator species known to occur at the sites were invasive feral cats, stoats and weasels (*Mustela nivalis*) as well as self-introduced Australasian harriers (*Circus approximans*) and native New Zealand falcons (*Falco novaeseelandiae*).

Rabbit abundance and poisoning

An index of rabbit abundance was measured at each site by counting rabbits with spotlights from the back of a vehicle travelling at 10-15 km/hr along fixed 9-13 km transects. The same transects were resampled over three consecutive nights, with sampling sessions occurring approximately every 16 weeks. The only change in observer was a permanent change between July 1994 and October 1994 at Earnscleugh. Rabbit abundances at the beginning of the study were between 83 and 155 rabbits per km of spotlight transect. This level of infestation has been previously classed as 'extreme' (> 40 rabbits/spotlight km; Kerr et al. 1987).

Rabbits were poisoned at the two treatment sites in September 1994 with sodium monofluoroacetate (1080) which was aerially distributed via diced carrot (20-30 kg of carrot/ha) at a concentration of 0.02% wet weight. While we refer to the periods before and after poisoning as 'pre-control' and 'post-control', low-level rabbit control (occasional shooting) occurred at both treatment sites post-poisoning.

Ferret density

To estimate population densities, ferrets were live-trapped over four consecutive nights at each site every 4-6 weeks between March 1994 and May 1996. In each trapping session 60-70 cage traps, each with a fresh rabbit meat lure, were set at permanent locations spaced 300-400 m apart along vehicle tracks. All traps were checked once daily, non-target species were released, and traps were rebaited as necessary. Any new ferrets captured were sexed (assessed external genitalia) and marked with a uniquely identifying ear tag, and recaptures of any previously tagged ferrets (from the current or a previous trapping session) were recorded.

For each trapping session we estimated population density by spatially-explicit mark-recapture analysis using the program DENSITY (Efford et al. 2004). Previous analysis of the first 11 capture-mark-recapture sessions (Norbury and Efford 2004) found that the maximum likelihood estimator for the null model M_0 yielded estimates with higher precision than was obtained using Chao's second coverage estimator for the model M_{th} (see Otis et al. 1978 for discussion of these models). We therefore took a conservative approach and chose the null model for ferret density estimation.

Numerical response of ferrets to declines in primary prey

Because rabbit and ferret surveys were not always conducted simultaneously at each site, we estimated the rabbit abundance at the time of each ferret survey by linear interpolation. For a small number of ferret surveys conducted between the last rabbit survey pre-control and the first rabbit survey post-control, it was not valid to estimate the corresponding rabbit abundances by interpolation, because rabbit abundance was not expected to decline until after baiting. In these instances, we estimated rabbit abundance using predicted values from the linear model of rabbit abundance survey data in the pre-control period. Because poisoned

rabbits remained in the landscape and continued to provide food for ferrets for a short period following baiting, we excluded data from any survey occurring during this 'carrion period' (designated as September-October 1994). A 2 month carrion period was selected based on previously documented rates of rabbit decomposition in the United States (De Jong and Chadwick 1999) and decomposition rates of possums in New Zealand (Meenken and Booth 2010). Given the high number of scavengers in this landscape, 2 months is probably an overestimate. Because of the limited number of rabbit and ferret surveys, particularly before baiting, we did not test for a lag period in the numerical response of ferrets to change in rabbit abundance. Incorporating a lag period would have required further exclusion of survey data from the autumn and winter sessions in 1994, in turn limiting the number of parameters we were able to estimate with modelling without increasing the risk of overfitting the available data.

We used linear models and multimodel inference to analyse the effect of rabbit abundance (estimated at the time of each ferret survey as described above), season (*autumn* = March-May; *winter* = June-July; *spring/summer* = September-February) and site on ferret density. For model comparison we ran 10 separate models, including a null model, three univariate models, all possible combinations of model with additive effects for each of the three predictor variables, and models with a rabbit abundance:site interaction and a rabbit abundance:season interaction (Table 1). Given sample sizes and the number of model parameters, we ranked all candidate models for each analysis using ΔAICc for small sample sizes (Burnham and Anderson 2002). All interpolation and modelling was conducted in R (R Core Team 2017) using the MuMIn package (Barton 2013) to rank and compare models.

Scat analysis

When available, freshly-deposited ferret scats were collected from all traps. However, for ferrets that were caught on several nights within a session, the rabbit component of scats collected after the first night was excluded from analyses as this may have represented rabbit eaten as bait on the previous night. Scats were soaked in water overnight, washed in a 250 µm sieve, and the contents of each scat macroscopically sorted into different prey taxa (i.e., rabbit, lizard, bird, invertebrate, mouse, hedgehog, weasel/stoat, possum and cat).

We used percentage frequency occurrence per scat (hereafter 'frequency of occurrence') to compare the diet of ferrets spatially (site differences) and temporally (pre-control period, 6 months post-control, and 18 months post-control). We expressed the frequency of occurrence *F* of a given food item *i* in any given sampling session *j*, as the number of scat samples within that session in which the food item occurred N_{ij} divided by the total number of samples containing identifiable contents, multiplied by 100:

$$F_{ij} = \left(\frac{N_{ij}}{N_j}\right) \text{ x } 100.$$

Frequency of occurrence is the most commonly used method of quantification in scat analyses and is recommended when data on the volume, mass or numbers of diet items in the scat are unavailable (Klare et al. 2011).

While it was not possible to accurately count the number of individuals of mammalian and avian prey, we obtained individual count data for lizards and invertebrate prey. For lizards we counted the number of undigested left and right front or hind feet in any scat containing lizards and used the highest count (divided by four) to estimate the minimum number of lizards per scat. For invertebrates, we counted the number of individual undigested exoskeletons which could be allocated to a single individual. For lizards and invertebrates, we calculated the number of individuals per scat per sampling session as the sum of individuals of a given prey item *i* within a sampling session *j* divided by the total number of scat samples containing identifiable contents collected during that session N_j:

$$\text{Individuals per scat} = \frac{\sum individuals_{ij}}{N_j}$$

Because maggots were likely to have been ingested incidentally though scavenging, rather than a targeted prey item, we omitted all maggots from our analyses.

Functional and total response of ferrets to declines in primary prey

We tested for an increase in consumption of secondary prey species in response to fewer rabbits by comparing the frequency occurrence of primary and alternative prey items, and the mean number of individuals per scat of lizards and invertebrates, between three periods: autumn (March-May) in 1994 (pre-control), autumn 1995 (6 months post-control) and

autumn 1996 (18 months post-control). The analysis was restricted to autumn as this was the only season where data were available before control and in multiple years post-control.

We used linear models to calculate *impact functions* which described the change in lizard and invertebrate consumption as a function of declining rabbit abundance. This involved standardising rabbit reductions across sites in the post-control period (or equivalent period for the non-treatment site) against the sites' average rabbit abundance for autumn in the pre-control period (or equivalent for the non-treatment site). Positive impact functions (or positive linear slopes) indicate lower consumption of alternative prey species when rabbit abundance is reduced. The reverse is true of negative impact functions, where higher consumption of alternative prey occurs when rabbit abundance is reduced.

We modelled impact functions for both the *per capita* and the *total response* of ferrets to rabbit declines. The *total response* of predators is the product of the numerical and functional response of predators (Pech et al. 1992) and was calculated here by multiplying the *per capita* response by the estimated ferret density for each survey period. Because ferret density was estimated as individuals per hectare, and because a single ferret scat is likely to represent ferret consumption over no more than 24 hours (potentially only 1-3 hours (Bell 1996)), this *total response* provides an estimate of the number of individual lizards or invertebrates consumed ha^{-1} day^{-1}. These analyses were again restricted to autumn so the responses were comparable.

RESULTS

Numerical response

Estimates of rabbit and ferret abundance during the pre-control period were highly variable among sites (Fig. 1). Rabbits were most abundant at Grays Hills, where spotlight surveys in April 1994 estimated 156 rabbits/km, more than double the peak values for Bendigo and Earnscleugh. Yet, pre-control ferret densities at Grays Hills were the lowest estimated, averaging 2.37 ferrets/ha in autumn 1994 compared to 4.9 ferrets/ha at Bendigo, and 2.8 ferrets/ha at Earnscleugh.

Baiting reduced rabbit abundance at both treatment sites (Fig. 1): averaged autumn estimates for the 1995 and 1996 surveys post-control were 82% lower the pre-control 1994 values at Bendigo, and 98% lower at Grays Hills. There was a 31% decrease in rabbit abundance over the same period at the non-treatment site (Earnscleugh). Ferret density declined over the same periods by 50% at Bendigo and 71% at Grays Hills and increased by less than 1% at the non-treatment site.

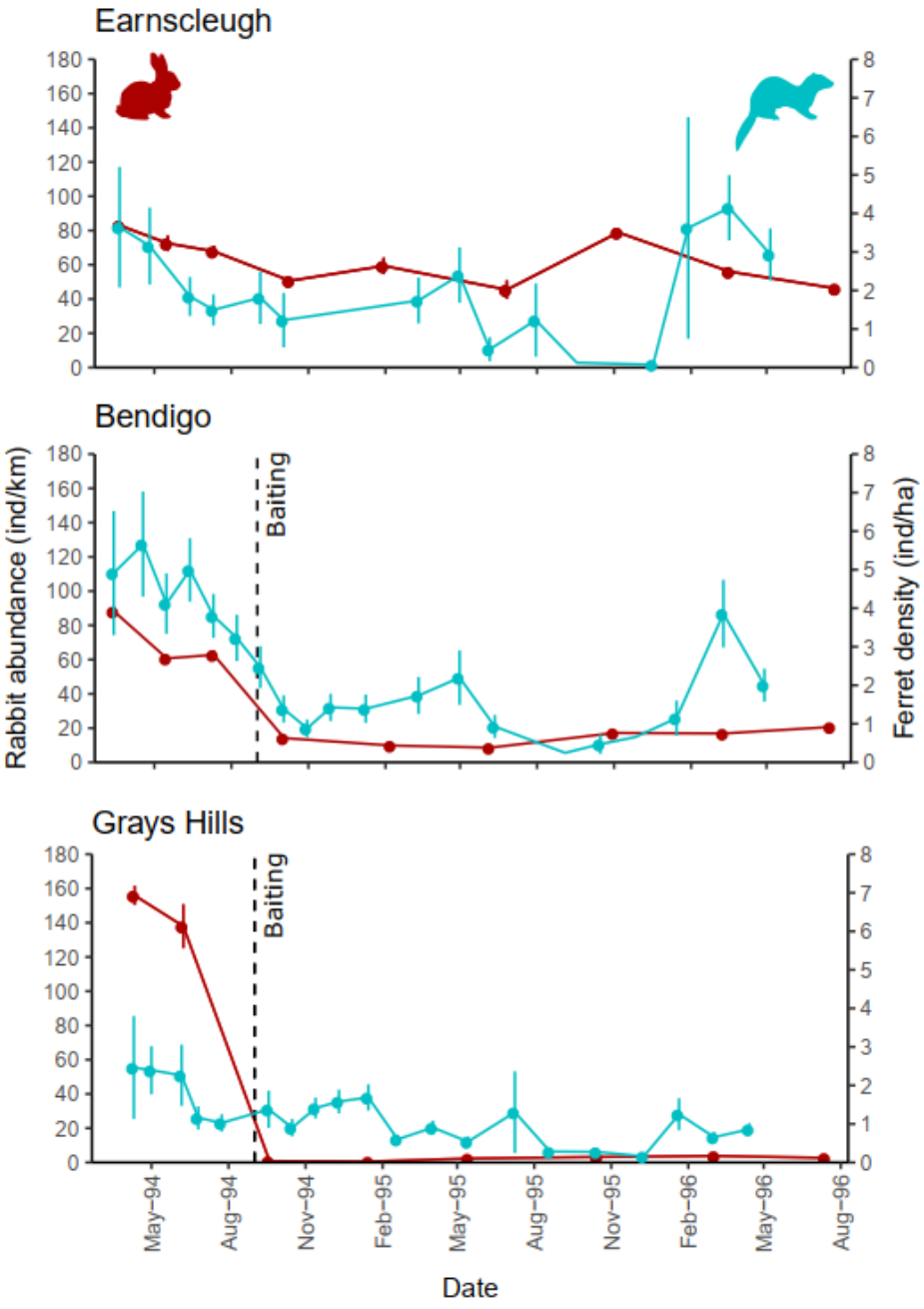

Fig. 1. Changes in rabbit abundance (dark red) and ferret density (light blue) at each site. The dashed line indicates when rabbit control occurred at the two treatment sites.

There was only one competitive model selected for the numerical response of ferrets (Table 1). This model included parameters for the interaction between rabbit abundance and site and the main effects (model weight = 0.99; Table 1). The significance of this interaction was driven by a stronger positive effect of rabbit abundance on ferret density at Bendigo (effect size: 0.016 ± 0.031) than either Grays Hills (0.057 ± 0.008) or Earnscleugh (0.007 ± 0.002) (Table 2, Fig. 2).

Table 1. Model selection of linear models for the numerical response of ferrets. Models are presented in order of ascending AICc values. Included are the number of estimated parameters (*K*), the maximum log-likelihood (*lnL*), AICc values, AICc differences (Δ*AICc*), the model weight (*W*) and an indication of model fit (R^2).

Model	*K*	*lnL*	*AICc*	*ΔAICc*	*W*	R^2
*rabbit*site*	*7*	*-64.89*	*146.4*	*0.00*	*0.99*	*0.61*
rabbit + site + season	7	-70.16	156.9	10.54	0.01	0.52
site + season	6	-74.16	162.2	15.85	0.00	0.43
rabbit + site	5	-77.68	166.7	20.31	0.00	0.35
rabbit + season	5	-78.37	168.1	21.68	0.00	0.33
rabbit*season	7	-77.06	169.5	23.06	0.00	0.37
season	4	-80.29	170.7	24.33	0.00	0.28
rabbit	3	-84.61	175.7	29.33	0.00	0.15
site	4	-84.10	177.1	30.68	0.00	0.16
null	2	-88.65	181.5	35.16	0.00	0.00

Table 2. Parameter estimates for the best ranked model from the static numerical response model selection, including an effect for rabbit abundance, site, and a rabbit abundance:site interaction term.

Parameters	coefficient	s.e.	t-value	Pr(>|t|)
Intercept	0.86	1.421	0.60	0.55
rabbit	0.02	0.002	0.72	0.48
site (Bendigo)	-0.20	1.461	-0.14	0.89
site (Grays Hills)	-0.05	1.445	-0.04	0.97
rabbit:site (Bendigo)	*0.04*	*0.024*	*1.69*	*0.01*
rabbit:site (Grays Hills)	-0.01	0.022	-0.38	0.71

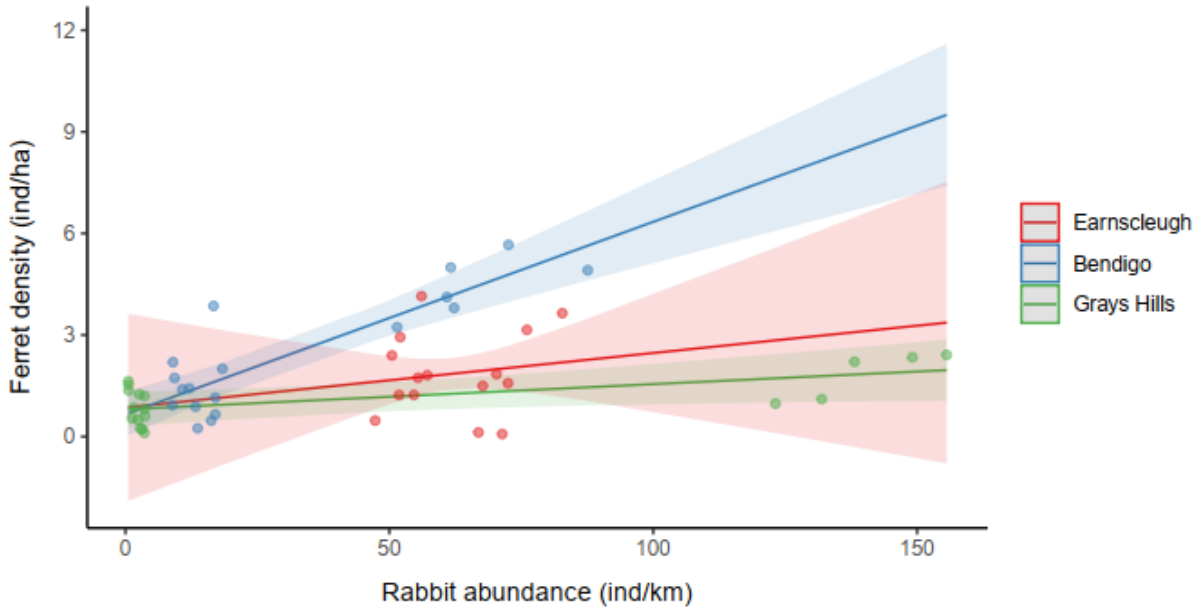

Fig. 2. Linear relationship between ferret density and rabbit abundance at each site (95% confidence intervals indicated by shading).

Functional response

Rabbit was the most frequent prey item in ferret scats, occurring in 86% of scats collected over the study period (Table 3). The next most frequently occurring prey were lizards (25%), followed by invertebrates (14%), birds (including eggs; 8%), and finally non-rabbit mammalian prey (6%). Even when rabbits were barely detectable in spotlight surveys (e.g. average abundance estimates of 0.7 rabbits/km at Grays Hills in the post-control period), the frequency of occurrence of rabbit in ferret scats remained high, at 53% and 68% of scats in autumn 1995 and 1996, respectively (Table 4).

The frequency of occurrence of alternative prey items (i.e., non-rabbit prey) mostly increased at the treatment sites following rabbit control, while either decreasing (6 months post-control) or remaining unchanged (18 months post-control) at the non-treatment site (Table 4). In addition, there was a general trend for increased per capita consumption of lizards and invertebrates following baiting at the two treatment sites. This was most evident at Grays Hills, where rabbit control was most effective (Fig. 3).

Table 3. Summary of ferret scat analysis from three study sites.

Site	Earnscleugh		Bendigo		Grays Hills		Total	
	n	%	n	%	n	%	n	%
Sample size								
Scats collected	245	-	351	-	388	-	984	-
Scats with identifiable prey	215	88	293	83	353	91	861	88
Frequency occurrence[a]								
Rabbit	206	96	267	91	269	76	742	86
Lizard	26	12	64	22	122	35	212	25
Invertebrate	20	9	28	10	76	22	124	14
Bird/egg	7	3	16	5	46	13	69	8
Other mammal[b]	4	2	12	4	36	10	52	6
Lizards								
Total lizards consumed	55	-	114	-	337	-	506	-
Max. lizard/scat	12	-	14	-	19	-	19	-
Invertebrates								
Total invertebrates consumed	29	-	50	-	359	-	438	-
Max. invert/scat	4	-	7	-	37	-	37	-

[a] averaged across all sessions; [b] includes mouse, hedgehog, weasel/stoat, possum and cat

Table 4. Percent frequency of occurrence of primary (rabbit) and alternative (non-rabbit) prey items during autumn sessions (March – May) in 1994 (pre-control), 1995 (6 months post-control) and 1996 (18 months post-control).

Site	Earnscleugh		Bendigo		Grays Hills	
	n	%	n	%	n	%
Primary prey (rabbit)						
1994 (pre-control)	52	98	70	96	42	98
1995 (6 months post-control)	31	94	20	74	23	53
1996 (18 months post-control)	40	91	31	86	25	68
Alternative prey (non-rabbit)						
1994 (pre-control)	13	25	28	38	12	28
1995 (6 months post-control)	6	18	18	67	28	65
1996 (18 months post-control)	12	27	13	36	22	59

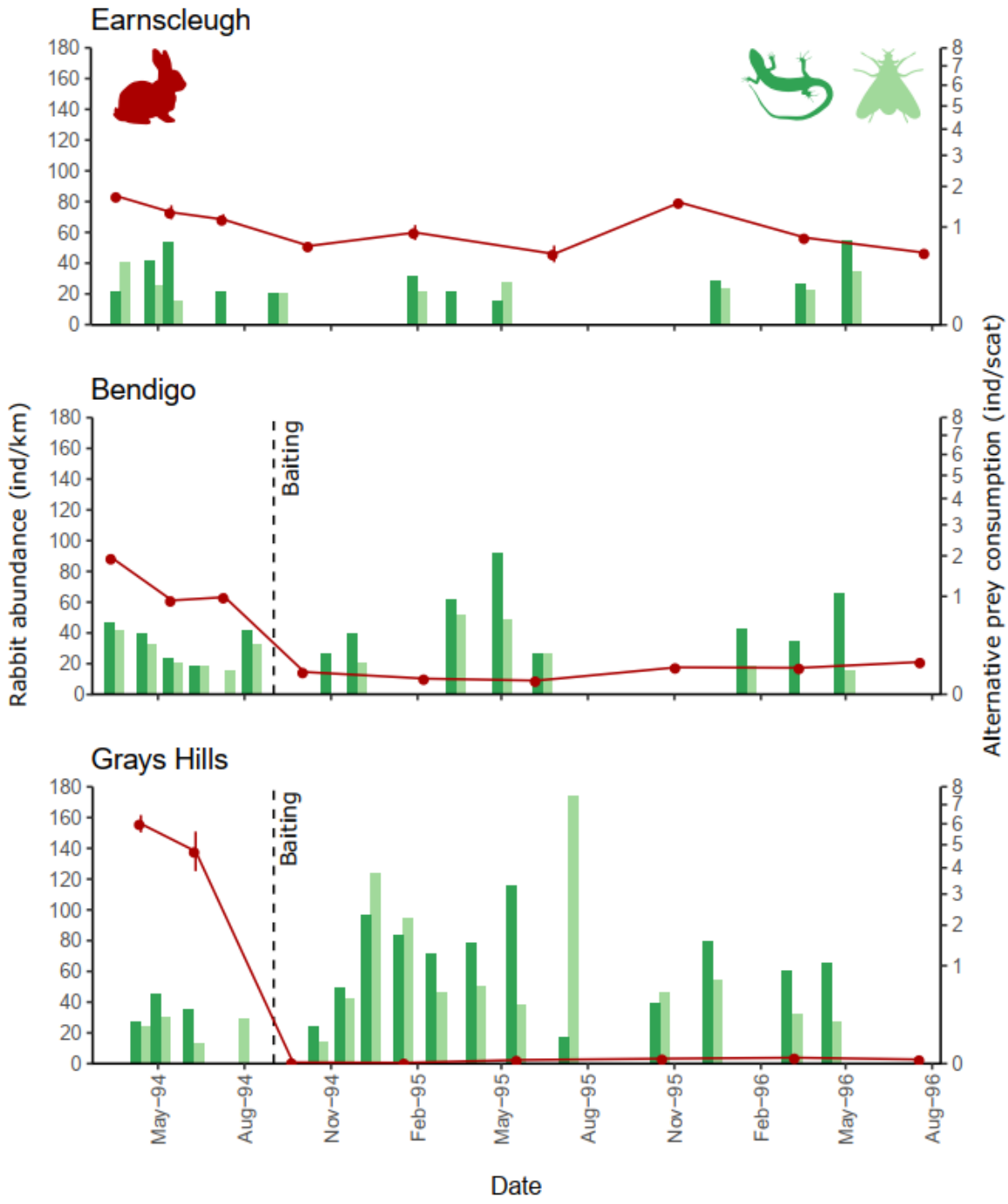

Fig. 3. Changes in alternative (non-rabbit) prey consumption (individuals/scat) at each site from 1994 to 1996. Lizard consumption is indicated by the dark green bars, and invertebrates by the light green bars. Rabbit abundance estimates (and standard error) are plotted for the same period. The dashed line indicates when rabbit baiting occurred at the two treatment sites

At the Bendigo treatment site, the average number of lizard and invertebrate individuals per scat increased by 336% and 152%, respectively, from autumn pre-control to autumn 6 months post-control. During the corresponding period at the Grays Hills treatment site, there was an almost 500% increase in lizards per scat and a 179% increase in invertebrates per scat, while at the non-treatment site (Earnscleugh) the number of lizards and invertebrates per scat decreased (Table 5). At both treatment sites there were fewer lizards and invertebrates per scat in the period 18 months post-control than in the period 6 months post-control, but consumption rates remained above pre-control levels (except for invertebrates at Bendigo) (Table 5). In contrast, at the non-treatment site the number of lizards and invertebrates per scat increased between 6 and 18 months post control (Table 5).

Linear impact functions were negative for per capita consumption (functional response) of lizards and invertebrates, again indicating prey-switching to alternative prey as rabbits became less available (Fig. 4a). This negative slope was steeper for lizards than for invertebrates, indicating that as rabbits became less abundant, ferrets preferentially consumed lizards (slope = -1.22) over invertebrates (slope = -0.14).

Table 5. Individuals per scat *(Ind/scat)* and mean predation pressure ± SE *(PP)* for lizards and invertebrates during autumn sessions (March – May) in 1994 (pre-control), 1995 (6 months post-control) and 1996 (18 months post-control).

Site	Earnscleugh		Bendigo		Grays Hills	
Lizards	*Ind/scat*	*PP*	*Ind/scat*	*PP*	*Ind/scat*	*PP*
1994 (pre-control)	0.42	0.96 ± 0.22	0.33	1.78 ± 0.50	0.35	0.81 ± 0.25
1995 (6 m post-control)	0.09	0.18 ± 0.02	1.44	3.09 ± 1.05	2.09	1.45 ± 0.11
1996 (18 m post-control)	0.43	1.45 ± 0.53	0.64	1.64 ± 0.34	0.95	0.70 ± 0.11
Invertebrates	*Ind/scat*	*PP*	*Ind/scat*	*PP*	*Ind/scat*	*PP*
1994 (pre-control)	0.21	0.70 ± 0.34	0.25	1.35 ± 0.39	0.19	0.44 ± 0.07
1995 (6 m post-control)	0.09	0.23 ± 0.16	0.63	1.22 ± 0.04	0.53	0.35 ± 0.12
1996 (18 m post-control)	0.20	0.71 ± 0.12	0.03	0.06 ± 0.04	0.22	0.15 ± 0.00

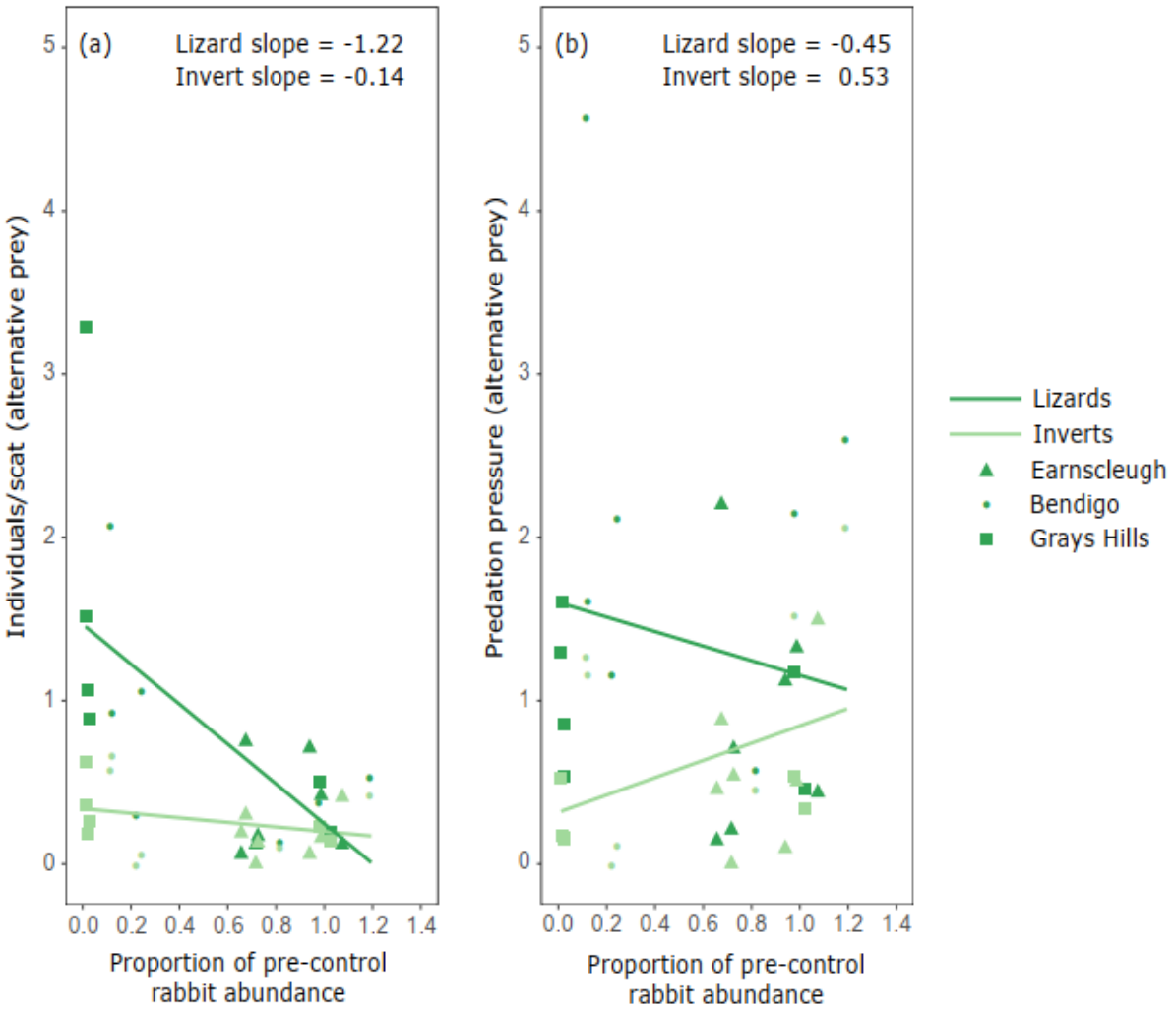

Fig. 4. Linear impact functions of rabbit reduction on (a) the estimated average number of secondary prey individuals per ferret scat during autumn (functional response), and (b) the estimated average number of individuals consumed by ferrets per hectare per day during autumn (total response). Reductions in rabbit abundance are compared to a baseline value where x = 1.0 represents the average rabbit abundance in autumn 1994 (pre-control period) standardised across sites. Therefore x = 0.6 represents a reduction in rabbit abundance to 60% of the sites average abundance in the pre-control period (or equivalent period for the non-treatment site). This analysis was restricted to autumn as this was the only season with estimates every year of the study

Total response

The slope of the impact function for the total response of ferrets was negative for lizards (-0.45) but positive for invertebrates (0.53) (Fig. 4b). Rabbit reductions therefore had a positive overall effect on invertebrates, as the positive impact of decreased ferret densities (numerical

response) more than offset the negative impact of the increased per-capita consumption of invertebrates (functional response), but not for lizards. However, the increase in predation pressure on lizards was generally limited to the 6 month period post-control (Table 5).

DISCUSSION

Ferrets responded to rabbit control both numerically and functionally. As predicted, decreasing rabbit abundances led to decreased ferret densities and increased per capita consumption of alternative prey species, particularly 6 months following rabbit declines. The net effect of rabbit control was negative for lizards in the short term (6 months post-control), as prey-switching by ferrets led to increased predation pressure, but became more positive with time post-control. These results suggest that rabbit control alone is a risky strategy to protect native lizards in this system.

Numerical response

There was support for a numerical response of ferrets to rabbits: ferret densities generally decreased as rabbits became less abundant. This supports previous suggestions that population dynamics in New Zealand's drylands are driven by 'bottom-up' processes, and that in these regions rabbit control can be an effective means of reducing predator abundance (Norbury and Jones 2015). It also supports findings from a broader range of habitats and predator species, showing declines of cats and foxes in Australia following rabbit control (Bowen and Read 1998, Mutze et al. 1998, Holden and Mutze 2002, but see Scroggie et al. 2018), and that rabbit density partially regulates fox (Ferreras et al. 2011) and eagle owl (*Bubo bubo*) populations (Fernández-de-Simón et al. 2014) within the native range of rabbits in Europe.

While we found a positive numerical response of ferrets to rabbits at all sites, the strength of this response was variable. The strongest numerical response was observed at Bendigo where rabbit reductions were more moderate (82% reduction), rather than at Grays Hills where rabbit reductions were most dramatic (98% reduction). This suggests inherent site differences in factors regulating rabbit and ferret populations. Studies in other countries have also found this to be the case for rabbit and predator populations, even when sites are geographically

close (separated by less than 22 km) and appear to be ecologically similar (Banks 2000). These results highlight the unreliability of extrapolating numerical responses observed at a single site more broadly, and the difficulties of predicting pest control outcomes for other species in a complex ecological community.

Functional response

Previous studies of ferret diet have typically reported percentage frequency of occurrence of different prey items in scats or guts (Robertson 1976, Pierce 1987, Alterio 1994, Mills 1994, Smith et al. 1995, Ragg 1998, Murphy et al. 2004, Bodey et al. 2010). As for most diet studies of invasive ferret populations, we found rabbits were consistently the most frequently occurring prey species. At our non-treatment site the frequency occurrence of rabbits (95%) was higher than reported in any previous study from the Otago/Southland (Robertson 1976, Alterio 1994, Smith et al. 1995, Ragg 1998) or Mackenzie Basin (Pierce 1987, Murphy et al. 2004) regions of New Zealand, where rabbit frequency occurrence has ranged between 40% (Robertson 1976) and 87% (Ragg 1998). Even during the post-control period at both treatment sites, the frequency occurrence of rabbits remained higher than that reported in most previous studies. These results highlight the strength of ferrets' dietary preference for rabbits at these sites, and the ability of ferrets to locate rabbits at low densities, even when they are barely detectable in spotlight surveys (detections of less than one rabbit/km).

While rabbits remained a consistently targeted prey, there was clear evidence for prey-switching following rabbit control. This increase in consumption of non-rabbit prey was greater in the period 6 months following control than in the period 18 months following control. This suggests that the negative impacts of prey-switching are most severe in the period immediately following rabbit control and become less severe with time. Other studies have also observed prey-switching by generalist predators following sudden reductions in local rabbit populations. This has led to increased predation of invertebrates (Read and Bowen 2001, Holden and Mutze 2002), mammals (Molsher et al. 1999), reptiles (Norbury 2001, Sharp et al. 2002) and birds (Sharp et al. 2002, Moleon et al. 2008). Sudden rabbit declines have also been linked to increases in the nest predation of banded dotterels (*Charadrius bicintus*) (Pierce 1987, Rebergen et al. 1998, Norbury et al. 2002) and purple

swamphens (or pukeko, *Porphyrio porphyrio*) (Haselmayer and Jamieson 2001), as well as sudden declines in black stilts (*Himantopus novazelandiae*) (Pierce 1996).

Ferrets consumed more lizards than invertebrates in almost all sampling periods (Fig. 3). Lizards therefore faced a greater increase in predation risk than invertebrates in the short term following rabbit control. Other studies have found differential impacts on alternative prey species from prey-switching. For example, while Holden and Mutze (2002) found that cats increased their consumption of invertebrates following rabbit reductions, and Molsher *et al.* (1999) documented an increase in the consumption of house mice, neither study recorded an increase in the consumption of small native mammals, birds or reptiles. However, as we did not measure the relative availability of alternative prey species, it remains unclear if the predominance of lizards over invertebrates in the diet reflects a true 'preference' for lizards or differences in availability (Allen and Leung 2012). Additionally, previous studies have suggested that ferret diet varies seasonally in New Zealand, and that during autumn and winter ferrets consume fewer rabbits and more lizards and birds (Mills 1994, Ragg 1998). If ferret diet is similarly seasonal at our study sites, our results – which were restricted to autumn for reasons outlined in the methods – could represent the annual peak in predation pressure for alternative prey. The relative importance of lizard and invertebrate prey items may also shift seasonally. While we have scarce data for ferret diet in winter, scat contents from a July survey at Grays Hills demonstrate a far greater consumption of invertebrates relative to lizards (Fig. 3), possibly due to dormancy of New Zealand lizards during winter months (Barwick 1959). It is therefore possible that the impacts of prey-switching may have been greater for invertebrates in other seasons.

Total response

The total response (the product of both the numerical and functional responses) indicates that while declines in the abundance of ferrets following rabbit control offset the autumn increases in per-capita predation for invertebrates, they did not completely offset the short-term increase in predation for lizards. This is concerning as many dryland lizard species are threatened (Hitchmough et al. 2016) and long maturation periods and low reproductive outputs limit how quickly lizard populations can replace individuals killed by predators (Cree and Hare 2016).

Similar concerns surrounding removal of primary prey have been identified globally. For example, in Patagonia, the removal of domestic sheep (*Ovis aries*) led to rapid increases in predation of endangered huemel deer (*Hippocamelus bisulcus*) by several shared predator species (Wittmer et al. 2013a), and in North America sudden declines of white-tailed deer increased the predation of endangered woodland caribou (*Rangifer tarandus caribou*) by cougars (*Puma concolor*) (Serrouya et al. 2015). One option for limiting these negative impacts is to conduct simultaneous or near simultaneous predator control alongside primary prey control (Wittmer et al. 2013b, Bode et al. 2015). This strategy was adopted on California's Channel Islands after a modelling study (Courchamp et al. 2003b) indicated that only the simultaneous removal of feral pigs (*Sus scrofa*; the primary prey species) and golden eagles (*Aquila chrysaetos*; a shared predator) could ensure the persistence of endangered island foxes (*Urocyon littoralis*). Following the removal of pigs and eagles, fox populations have recovered rapidly (Coonan et al. 2014). These findings highlight the importance of understanding how controlling different invasive species can affect the prey species we seek to conserve, and the potential benefits of simultaneously controlling invasive predators and invasive prey. Despite this, simultaneous control is still rarely prescribed in management plans (Reddiex et al. 2006).

While the total response suggests that lizards are negatively affected by rabbit control in the short term, monitoring at our sites ended 20 months after rabbit control. It is possible that continued monitoring post-control may have revealed greater long-term benefits for alternative prey, as has been predicted by numerous modelling studies (Pech and Hood 1998, Courchamp et al. 1999, Lurgi et al. 2018). In arid Australia, positive total responses to rabbit control are the proposed mechanism for the recovery of four small mammal species with some species having an almost 70-fold increase in their extent of occurrence in the 14 years following rabbit suppression (Pedler et al. 2016). In demonstrating the benefits of rabbit control for native species, Pedler et al. (2016) stress the importance of long-term ecological monitoring and the fact that these patterns may have remained elusive if data collection had been more temporally limited. It is also important to note that alternative prey are likely to benefit from rabbit suppression in ways that are not necessarily represented by the short-term total response. For example, regeneration including increasing complexity of drylands vegetation occurs following reductions in grazing pressure from rabbits (Scroggie et al. 2013).

This increases food and refuge availability for prey (Norbury 2001), and reduces the hunting efficiency of remaining predators (Norbury and van Overmeire 2019).

Finally, while this study focussed on the total response of ferrets to rabbit control, rabbits are also the primary prey of other generalist predators including feral cats and several native raptors in New Zealand's drylands. Quantifying the total response of all predators will therefore be necessary to gain a complete understanding of the consequences of rabbit control for native prey.

Management implications

Our results demonstrate that targeted control of an invasive primary prey species without coincident predator control can disadvantage some, but not all, alternative prey species in the short term. This suggests that minimising any undesirable short-term effects will require predator control alongside control of primary prey. Ideally, predator control should be timed so that predators are already at reduced population densities when prey-switching to native prey species is most likely to occur, in this instance approximately 6 months following rabbit control.

Our results also suggest that highly fluctuating rabbit populations will be particularly damaging for native prey, given the lag in the numerical response of predators and the short-term negative effects of prey-switching. This means that managers should aim to suppress rabbits, or other abundant primary prey species, over longer time frames, a strategy which has been shown to benefit native prey elsewhere (Pedler et al. 2016). This highlights the importance of continued development of methods such as viral releases that have been proven to effectively suppress rabbits over long time periods (Mutze et al. 2014). While we were able to quantify total response of predators in the period up to 18 months post-control, a lack of monitoring beyond this limits our ability to infer the longer-term consequences of rabbit control. To effectively protect native species at risk of hyperpredation, we need to understand how they are affected by control actions. This can only be achieved through the continued collection of long-term monitoring data from control and treatment sites, before and after management actions (BACI design) and by collecting data in a way that allows direct quantification of the predators' total response.

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CHAPTER 4

General Discussion

4.1 Overview

Introduced species have had catastrophic consequences for native fauna and ecosystems globally, but especially in island systems where they have been identified as the primary driver of extinction and endangerment of species (Doherty et al. 2016, Spatz et al. 2017). New Zealand is one such island system. Here, the human-facilitated introduction of eight terrestrial mammalian predators within the last ~800 years has had devastating impacts on New Zealand's native wildlife (Blackwell 2005). Introduced mammalian predators have undoubtedly contributed to the current conservation crisis, whereby the majority of New Zealand's highly endemic, extant, native and non-vagrant bird and reptile species are listed as either 'threatened' or 'at risk' (Hitchmough et al. 2016, Robertson et al. 2016).

Despite New Zealand's strong historical and ongoing commitment to alleviating the harmful impacts of introduced mammalian predators (Russell et al. 2015), current understanding of the mechanisms which make New Zealand's native prey so vulnerable to these predators remains limited. To help address this gap, this study aimed to better understand the extent to which two key threats; (i) prey naivety and (ii) hyperpredation, contribute to the heightened vulnerability of native lizards in New Zealand's dry grassland habitats (drylands). This research has also enabled reflections on how two current conservation strategies – predator exclusion and control of a primary prey species (rabbits) – affect populations of native prey and has highlighted potential avenues for future research.

4.2 Summary of key results

I found that a population of McCann's skinks (*Oligosoma maccanni*), a commonly occurring and non-threatened dryland lizard species, reduced basking frequency in the presence of feral cat cues. This indicates that at least one species of New Zealand lizard has rapidly gained the ability to recognise the threat posed by cats, a species introduced ~150 years ago. However, I also found that skinks that have experienced recent reductions in predation pressure (through the exclusion of mammalian predators via fencing) failed to discriminate feral cat cues as well as raptor cues, despite both evolutionary and ecological experience with avian

predators. This highlights the complexity of antipredator behaviours and indicates that predator avoidance by skinks is flexible, being affected by background predation pressure and fitness trade-offs.

As far as predator ecology is concerned, I also analysed the response of ferrets to a rabbit baiting operation at two dryland sites and found that large reductions in rabbit numbers led to decreased ferret densities. However, I also found that reduced availability of rabbits meant that surviving ferrets increased their per capita consumption of lizards, particularly in the period about 6 months post-baiting. The negative effects of prey-switching overwhelmed the positive effects of reduced predator densities, leading to short-term increases in total predation pressure for dryland lizards. This indicates that rabbit control in the absence of predator control is a risky strategy for protecting native prey in dryland environments, at least in the short term.

4.3 Implications for the future of New Zealand's lizard diversity

Some aspects of this research present a positive outlook for New Zealand lizard conservation. Particularly encouraging is the suggestion that at least part of New Zealand's lizard diversity recognises a recently introduced predator as a potential threat and responds to cues by reducing engagement in risky behaviours. This is especially encouraging given that previous studies have found little or no evidence that New Zealand lizards respond to introduced predator cues (Dumont 2015, Monks et al. 2019) and that other New Zealand species have been put forward as classic examples of naïve prey which fail to recognise or adopt any form of antipredator behaviour towards introduced predators ('level 1' naivety; Banks and Dickman 2007).

It was also encouraging to observe behavioural flexibility in lizards' responses to predator cues. This occurred as lizards from an area with a higher background risk of predation temporally targeted predator avoidance to periods of peak risk, while lizards from an area with a lower background risk of predation did not invest in predator avoidance, instead opting to maintain high levels of basking activity. Because predator avoidance has fitness costs (Lima and Dill 1990, Downes 2001), there are advantages to being able to adjust antipredator behaviours based on some measure of relative risk, and thereby minimise the non-consumptive effects of predation (Sih et al. 2010). In lizards, predator avoidance is associated

with reduced basking and foraging activity (Downes 2001). This leads to reduced body size (Downes 2001), and for viviparous lizards (99% of New Zealand's lizard species; Cree and Hare 2016), reduced clutch sizes (Holmes and Cree 2006), smaller offspring (Wapstra et al. 2010) and lowered offspring survival rates (Wapstra et al. 2010). The behavioural flexibility that I observed suggests that lizards do not prioritise predator avoidance over other essential activities (e.g. basking) to the point that the non-consumptive costs outweigh the benefits of avoiding potential consumption. This is especially important for species of conservation concern, given suggestions that the impacts of non-consumptive effects can be just as damaging as the impacts of direct consumption on prey demographics (Preisser et al. 2005).

Despite these somewhat encouraging findings, McCann's skinks along with other dryland lizard species, clearly remain a frequently consumed prey item for introduced species, including ferrets and cats (Chapter 3, Middlemiss 1995, Norbury 2001). While the ability to discriminate the cues of a predator is essential in enabling prey to mount an antipredator response (and overcome 'level 1' naivety; Banks and Dickman 2007), discrimination alone does not ensure that prey will be able to effectively evade predation or maintain viable populations in the presence of predators (Banks and Dickman 2007, Carthey and Blumstein 2018). For instance, even if the ability to recognise a novel predator is widespread amongst New Zealand lizards (something that remains to be tested), their response to these predators may continue to be inappropriate ('level 2' naivety; Banks and Dickman 2007). An example is if lizards adopt cryptic 'freeze' behaviours – an appropriate response for evading predation from visually-orientated predators such as birds or Tuatara (Meyer-Rochow and Teh 1991, Worthy and Holdaway 2002), but inappropriate against ferrets, cats and other introduced mammals that rely heavily on olfactory cues to locate prey (Conover 2007).

Even if New Zealand lizards respond appropriately to introduced predator threats (as is suggested in the case of McCann's skinks where we observed reductions in 'risky' basking activity) they will remain vulnerable if these defences are ineffective ('level 3' naivety; Banks and Dickman 2007). Ineffective defences can result from a wide array of intrinsic biological traits developed by New Zealand lizards in an environment free of mammalian predators. For example, long maturation periods (e.g. up to 8 years for some dryland geckos (Woodworthia 'Otago large')) and low reproductive outputs (e.g. average of 1.4-2.3 young female^{-1} year^{-1} in Otago Skinks *O. otagense*) limit the ability of populations to quickly replace individuals killed

by predators (Cree and Hare 2016). The activity phase of lizards may also limit how effectively lizards can avoid predation. For example, while we found that McCann's skinks responded to the visual cues of a predator, this response is of little use if predation is occurring at night when temperatures drop, and skinks are inactive. A recent study found some evidence that New Zealand's diurnal lizard species are more vulnerable to extinction than nocturnal species (Tingley et al. 2013), a result that could be linked to the large number of introduced mammalian predators that hunt primarily at night (King 1990). It is even possible that the body scent of New Zealand lizards may increase their vulnerability: a recent study finding that New Zealand birds smell stronger than continental birds, making them poorly adapted to defend against olfactory predators (Burford 2011). Until prey are able to recognise a predatory threat, as well as mount an appropriate and effective antipredator response, a positive conservation outcome remains unlikely, indicating that prey need further experience with focal predators to develop an 'optimal' response (Carthey and Blumstein 2018).

4.4 Reflections on current conservation strategies

Collectively, the results of this thesis highlight that multiple conservation strategies, currently utilised in New Zealand and globally, have unintended ecological consequences. Such findings are not unusual (Bergstrom et al. 2009, Ruscoe et al. 2011, Wittmer et al. 2013a, Jolly et al. 2018b, Muralidhar et al. 2019), particularly when dealing with highly invaded ecosystems (Zavaleta et al. 2001). These results reinforce the importance of understanding complex ecosystems, creating informed management plans, and conducting rigorous long-term monitoring to assess how conservation strategies affect target, as well as non-target species and ecosystem processes.

4.4.1 Predator exclusion

Mitigating the impacts of invasive predators at a landscape scale is an ongoing conservation challenge. In the interim, managers are increasingly seeking to conserve prey populations by excluding predators from smaller areas, such as offshore islands or fenced reserves. So far, invasive predators have been eradicated from over 1,000 small islands globally (Keitt et al. 2011), and further islands are continually being considered for eradication programs (e.g. Ringma et al. 2018). In mainland environments, the creation of predator-free reserves is achieved using exclusion fencing, an approach that has been particularly popular in

Australasia (Hayward and Somers 2012). Currently, New Zealand has at least 24 fenced reserves and Australia has at least 17, with further fenced reserves planned or under construction in both countries (Burns et al. 2012, Ringma et al. 2018, Innes et al. 2019). Despite the widespread adoption of localised predator exclusion, and its clear success in increasing the abundance of a wide range of threatened taxa (Towns et al. 2001, Innes et al. 2012, Legge et al. 2018), the long-term utility of this conservation strategy remains questioned (Scofield et al. 2011, Towns et al. 2016). One of the key concerns is that predator exclusion can reduce the resilience of prey by encouraging naivety, and therefore limit the potential for future co-existence between prey and predator populations (Hayward and Kerley 2009, Moseby et al. 2016). Some of the results from this study support these concerns, as they indicate that the exclusion of mammalian predators has increased the naivety of skinks within a fenced reserve (Chapter 2). While this increase in naivety does not appear to be problematic currently, and the fenced area supports a much higher density of skinks than adjacent high-predator areas (Wilson et al. 2017), it may become problematic in the future if this population of skinks experiences increased predator exposure, as can occur via predator incursion (e.g. Muralidhar 2017) or is a source population for re-introductions into areas with higher predation pressure (Jolly et al. 2018a, Jolly et al. 2018b).

Our results highlight the potential benefits of alternative strategies which offer some protection for prey populations, while also maintaining low levels of exposure to relevant predatory threats, and thereby enable prey populations to gain or maintain an antipredator response via learning, evolution through natural selection, or both (Moseby et al. 2016). This could occur by either intensively controlling predators over large areas, so that they remain at very low densities (e.g. Reardon et al. 2012, Glen et al. 2019), or through the controlled release of a small number of desexed individual predators into an otherwise predator-free area (e.g. Moseby et al. 2018a, West et al. 2018). Previous studies have demonstrated that these ‘low predator-exposure’ strategies can: (i) reduce predation to levels where even highly vulnerable prey species are able to persist or grow (Reardon et al. 2012, Moseby et al. 2018a); and (ii) increase the wariness and survival of threatened prey populations (Ross et al. 2018, West et al. 2018). These findings suggest that these methods can protect threatened species populations while enabling prey to further develop or maintain their antipredator responses. They also highlight the potential utility of ‘leaky' exclusion fences which exclude most but not

all introduced predators, and are more cost effective than impermeable exclusion fences when fenced areas are greater than 1 ha (Norbury et al. 2014, Moseby et al. 2018b). While these 'low predator-exposure' strategies may benefit conservation efforts in the long-term, we acknowledge that it may be inappropriate for protecting species where extinction risk remains high even with minimal predation risk (e.g. Grand skinks *O. grande*; Reardon *et al.* 2012), and the high economic costs of maintaining low predator densities in perpetuity (Clapperton and Day 2001).

4.4.2 Control of a primary prey species (rabbits)

While suppressing or eradicating introduced prey is often viewed as a potential mechanism to reduce the impacts of introduced predators on native prey (Courchamp et al. 1999, Cruz et al. 2013, Serrouya et al. 2015, Norbury 2017), it may also be a risky strategy. This research revealed short-term negative impacts for native and threatened prey following rabbit control (Chapter 3). Abundant rabbit populations not only have ecological costs, but significant economic costs, and are estimated to cost the New Zealand economy $60 M in production losses annually (adjusted for inlflation to 2019; Giera and Bell 2009). These costs mean that rabbit control will remain a key priority in New Zealand's drylands and in similarly affected landscapes globally (e.g. arid and temperate regions of Australia, parts of Chile and Argentina). The challenge for managing rabbit-infested landscapes is to maximise the economic and ecological benefits of rabbit-control across the whole ecosystem. If native prey are being negatively impacted by rabbit control, we need to build this knowledge and mitigating steps into future management plans. While this research demonstrated the potential risks associated with rabbit control, these concerns are equally applicable to the control of other prey species in any system where hyperpredation can occur, with previous studies noting similar challenges related to the removal of rodents (Murphy and Bradfield 1992), pigs (Courchamp et al. 2003b), sheep (Wittmer et al. 2013a) and moose (Serrouya et al. 2015).

One management strategy likely to improve outcomes for native prey species involves simultaneous or near-simultaneous predator control alongside rabbit control, at least in the initial phase of reducing rabbit abundance in a long-term suppression program, a process which limits the number of individual predators 'prey-switching' onto native species as rabbits becomes less available (Courchamp et al. 1999, Wittmer et al. 2013b, Bode et al. 2015).

Simultaneous control of predator and prey species has been highly successful in protecting threatened native prey in other systems (Coonan et al. 2014), and yet remains under-prescribed in management plans (Reddiex et al. 2006) due to technical, financial and/or social constraints. The results of this research support integrating predator control into rabbit control programs, and perhaps incentivising farmers or recreational hunters to target predators as well as rabbits when baiting or shooting at local scales. Secondly, actions that limit short-term fluctuations in rabbit abundance and instead keep populations continually suppressed over long time periods will benefit native prey, through reducing the frequency of damaging 'prey-switching' transition periods. This is perhaps most easily achieved though release of diseases such as rabbit haemorrhagic disease virus (RHDV), which has suppressed rabbit populations for ~ 8 years in some areas (Mutze et al. 2014). By using an integrated approach and combining forms of biological control with other control methods, rabbits can be further supressed over long time periods (Cooke et al. 2010). This highlights the importance of funding further research and development for new viral strains (as rabbits gain resistance) and providing a steady stream of resources to keep rabbit populations at low, stable levels using alternative control methods.

Finally, this research demonstrated that the effects of rabbit control are spatially and temporally variable, with predators responding differently to rabbit control depending on location, and the changing impacts of predators on alternative prey through time (Chapter 3). This finding further encourages funding and support for research that improves our understanding of species interactions before implementation of control (Caut et al. 2008), as well as for long-term monitoring of system dynamics post-control (Courchamp et al. 2003a, Pedler et al. 2016). By rigorously collecting empirical data related to management interventions in both the pre- and post-control periods, we can improve the reliability of simulation models that can be used to predict the outcomes of different management strategies (e.g. Tompkins and Veltman 2006, Lurgi et al. 2018). This will benefit conservation by reducing the significant risks and sunken-costs related to managing complex systems without first understanding them.

4.5 Recommendations for future research

While this research addressed several questions related to predator recognition by New Zealand lizards ('level 1' naivety), many questions remain. These include the extent to which a wider diversity of New Zealand's lizards recognise novel predators as a threat (this would be particularly interesting to test in relation to more highly threatened species, e.g. Grand and Otago skinks), as well as whether McCann's skink's recognition of cat cues extends to recognition of New Zealand's other introduced predators. To improve our understanding of prey-naivety in all its forms, further research should also address the extent to which 'inappropriate' or 'ineffective' antipredator responses ('level 2' and 'level 3' naivety) are contributing to the vulnerability of New Zealand prey. Finally, gaining an understanding of the mechanisms that underpin the gain and loss of predator recognition, such as the relative contributions of rapid evolution and/or learning, requires further testing, but is important in determining the likely prognosis for prey persistence (Carthey and Blumstein 2018).

In addressing potential issues surrounding rabbit control, future research should seek to understand whether dryland rabbit control facilitates mesopredator release of rats and mice, via reductions in predator abundance. Although this avenue of research has been previously suggested (Norbury 2001), it remains to be explored. Recent modelling of rabbit removal within an alternative system, indicated that reductions of 30-40% were optimal for native prey population growth (Lurgi et al. 2018). Given that rabbits were reduced by more than 80% at both study sites in this thesis (Chapter 3), and managers typically aim for the highest reductions possible, it would be interesting to explore how native prey might respond to less severe rabbit reductions in the dryland context.

Finally, increasing habitat structure (and the associated increases in refuge availability) is a potential management strategy for protecting native prey (Doherty et al. 2015), and can be achieved, in part, through rabbit removal or suppression (Scroggie et al. 2013, Schweizer et al. 2016). Previous studies have demonstrated that increases in habitat structure are linked to increases in prey survivorship (Norbury and van Overmeire 2019), reductions in predator hunting efficiency (McGregor et al. 2015), and higher prey fitness through reductions in the non-consumptive effects of predation (Arthur et al. 2004). Given these findings, dryland conservation would continue to benefit from research addressing (i) how rabbit abundance

influences habitat structure, and (ii) how habitat structure mediates both the consumptive and non-consumptive impacts of introduced predators on native prey.

4.6 Conclusions

As the number of threatened species reaches levels unprecedented in human history and the resources allocated to protecting them remain limited, effective and efficient conservation is an enormous challenge globally. Often conservation management is occurring in heavily modified systems, where native species are threatened by multiple introduced species, and species-interactions are complex and dynamic. By improving our understanding of how species interact within the ecosystems we seek to restore, we can better identify threats and better predict the outcomes of management interventions. This research has contributed to our understanding of interactions between native lizards and introduced predators in New Zealand's dryland habitats. My results suggest that at least one species of New Zealand lizard can recognise the threat associated with a novel predator. However, they also suggest that predator recognition can be rapidly lost following reductions in predator exposure. Introduced prey species also affect interactions between native prey and introduced predators. In New Zealand's drylands, abundant rabbit populations support higher ferret densities, which can lead to increased predation pressure for lizards, particularly during periods where rabbits are less available and ferret densities remain high (such as immediately following rabbit control). Collectively, these results highlight that interactions between native lizards and introduced predators are temporally and spatially variable. They also suggest that some of the current management strategies surrounding predator exclusion and rabbit control can have unintended, negative consequences – the impacts of which should be carefully considered moving forward.

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APPENDICES – CHAPTER 2

Appendix S1.

Fig. S1. The vegetation structure at the source site for (a) the 'high-predator' skink population – the 'Golden Point' Department of Conservation (DOC) reserve and (b) the 'low-predator' skink population – one of the DOC managed mammal-exclusion fences at Macraes Flat (photos: Hannah Cliff/Bart Biemans).

Appendix S2.

Animal husbandry

All skinks were acclimated to the laboratory for a minimum of 5 days (group 1) and a maximum of 26 days (group 4) prior to commencing behavioural trials. Each population was split into eight groups for housing, with four individuals of the same sex in each group (females groups 1-4 and males groups 1-4). Each group was housed in a 60L clear plastic terraria (W45 cm x L64 cm x H34 cm), with a 5 cm deep sand/pebble substrate (builders pre-mix). Each terraria had a warm retreat/basking site (terracotta saucer, 11cm diameter), situated 20 cm directly beneath a 42W halogen lamp, a cool retreat site (9.7 cm x 15.2 cm wooden refuge with 1.2 cm gap height), and an area of vegetative cover (moss). Water was provided *ad libitum* and lizards were fed every 2-3 days on a combination of cut fruit (apricot/mango), pureed fruit mixed with protein powder, and mealworms dusted in Calcium powder. Laboratory photoperiod was set to 12 h light (starting 08:00 h) and 12 h dark (starting 20:00 h). Basking lights in all housing terraria and the testing arenas were on for 7 h/day (09:00-16:00 h).

Appendix S3.

Further details of experimental treatments

On each 'procedural control' day:

1) All basking sites were associated with clean non-scented towelling (approximately 4cm wide, washed twice at 55˚C without detergent and air dried) which were placed on the tiles the previous evening;
2) An empty cage (L60cm x W26cm X H30cm) was placed in the centre of each arena for 32 minutes each morning (1h after the basking lights came on) and 32 minutes each afternoon (4h after basking lights on);
3) A pulley system running approximately 1.4 m above the arena substrate, was moved by a hidden operator five times within a 26 minute period, once in the morning (arena 1: starting 1h 5m after basking lights on; arena 2: starting 1h 35m after basking lights on) and again in the afternoon (arena 1: starting 5h 5m after basking lights on; arena 2: starting 4h 35m after basking lights on).

Each of the above 'standard procedures' were also followed on all treatment days, but with the following alterations.

1) *Cat scent treatment:* Four basking sites in each arena (two 'high refuge' sites at one end of the arena and 2 'low refuge' sites at the opposing end) were associated with towelling impregnated with cat body scent (towelling was placed in with bedding of two cats for one week, and frozen in a glass container for up to 10 days at -18˚C before use), all other basking sites were associated with non-scented towelling identical to those used in the control procedure.
2) *Cat treatment*: The cage placed in the centre of the arena housed one of two black female feral cats, the individual cats were used in alternate arenas between the morning and afternoon exposure sessions.
3) *Raptor treatment*: A taxidermy Australasian Harrier mounted in an attacking position was attached to the pulley system.

Appendix S4.

Fig. S4. Camera trap image of two basking skinks with clear identifying marks.

Appendix S5.

Table S5. The 15 candidate models used for model selection. Model 1 represents the null model and includes fixed and random effects which we expected to contribute variation to our data, but that were not of primary interest to our research questions (*arena* = testing arena 1 or 2, *t.day* = testing day 1-4 for each group, *temp* = mean maximum temperature (27-33˚C) of basking sites within each arena on a given day, *group.pen* = a random effect for the testing group each skink was from, *ID* = a random effect for each individual skink, *OD* = an observation level random effect (to account for data over dispersion). Models 2-15 build on the null model by adding additional terms of specific interest, including effects for population (*P*), treatment (*Tr*), sex (*S*) and interactions between population and treatment, and treatment and temperature.

Model	Model specification
1	Null = ~ 1 + arena + t.day + temp + (1|group.pen) + (1|ID) + (1|OD)
2	Null + P
3	Null + Tr
4	Null + S
5	Null+ P + Tr
6	Null + P + S
7	Null + Tr + S
8	Null + P + Tr + S
9	Null + P + Tr + P:Tr
10	Null + P + Tr + P:Tr + S
11	Null + Tr + Tr:temp
12	Null + P + Tr + Tr:temp
13	Null + P + Tr + Tr:temp + S
14	Null + P + Tr + P:Tr + Tr:temp
15	Null + P + Tr + P:Tr + Tr:temp + S

Appendix S6.

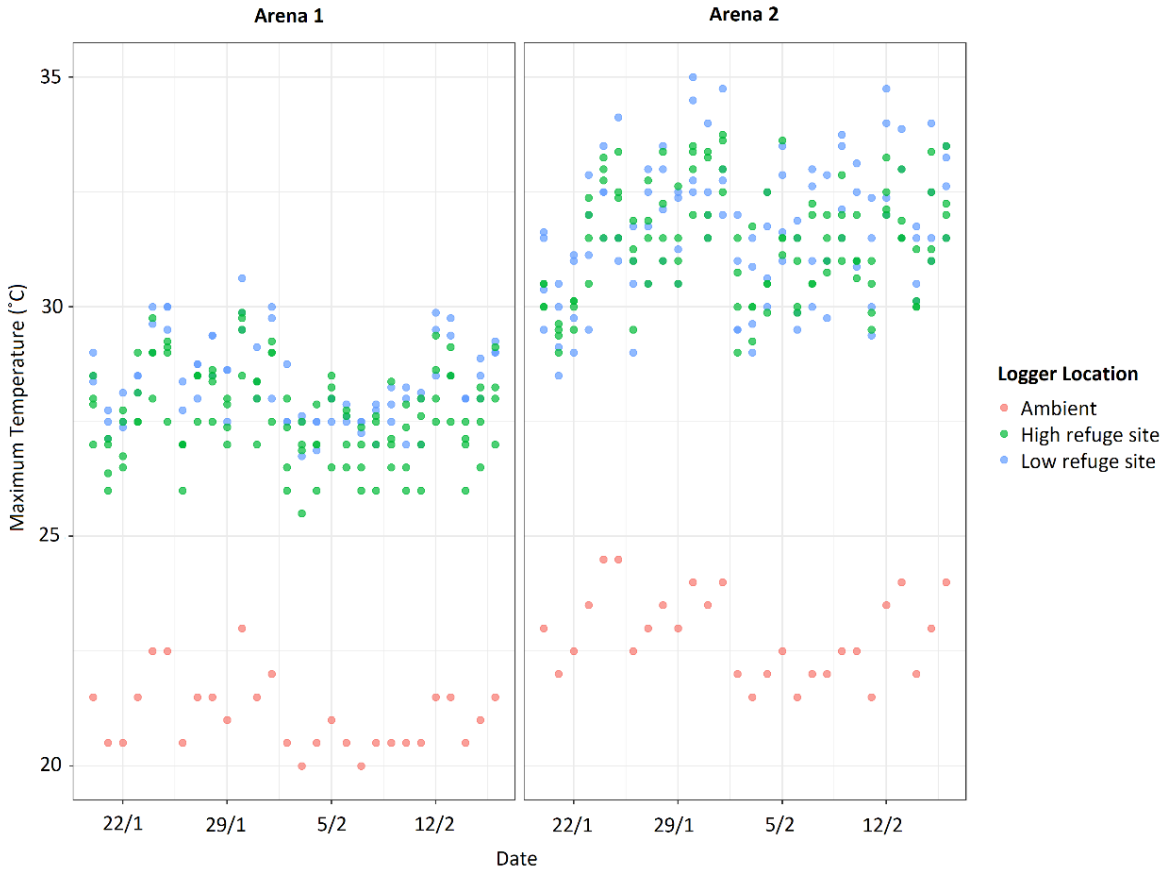

Fig. S6. Daily maximum temperature recorded by the ambient temperature logger (red) as well as each high-refuge (green) and low-refuge (blue) basking site within each testing arena over the duration of the study.

Appendix S7.

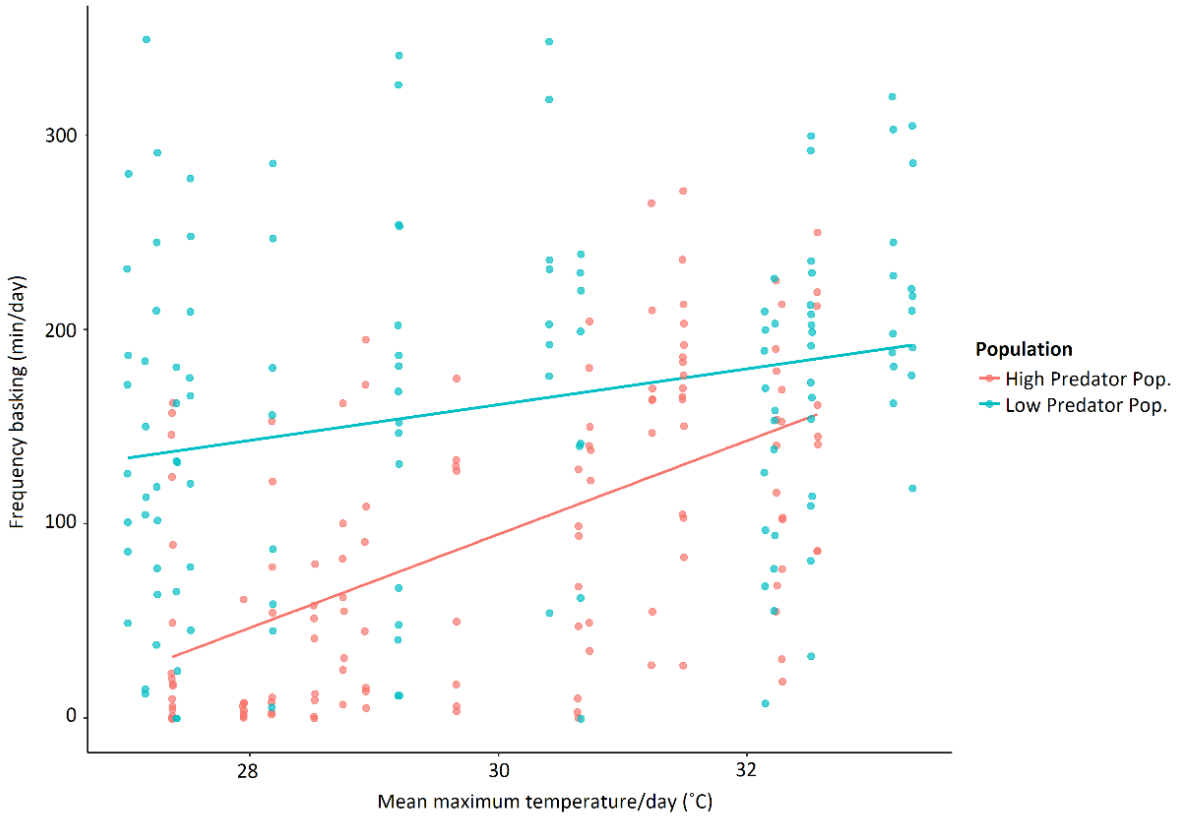

Fig. S7. Relationship between temperature of the basking tiles and frequency of basking for both the high-predator (red) and low-predator (blue) population.

Appendix S8.

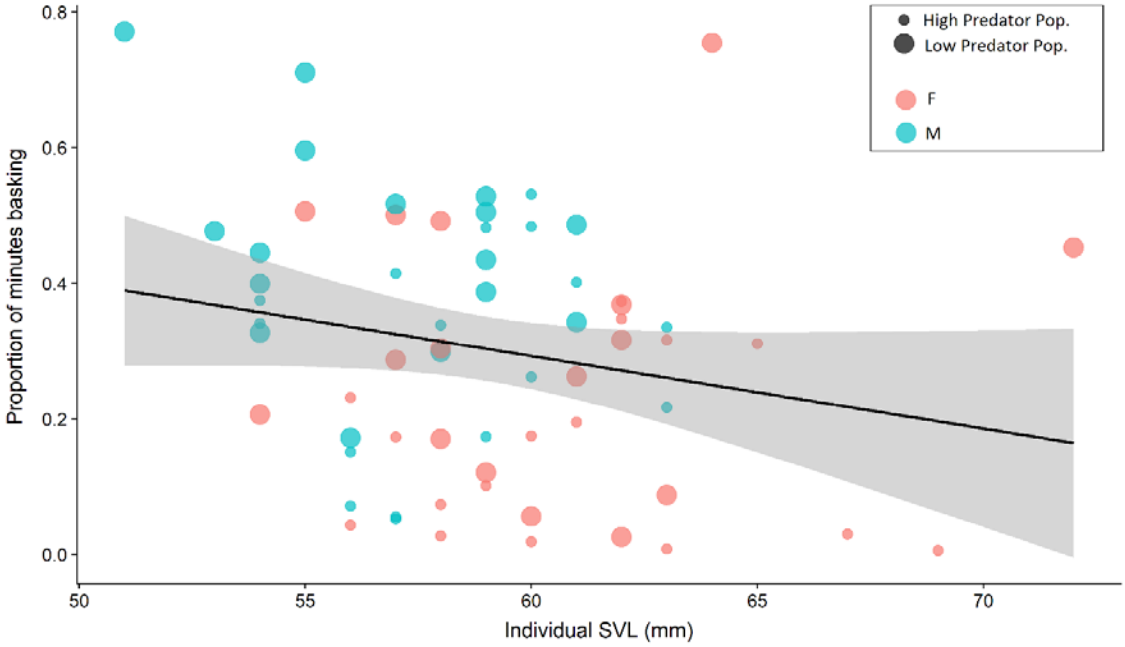

Fig. S8. The non-significant relationship between individual basking frequency (mean across four treatment days) and snout-vent length (SVL). Plot includes the line of best fit ($y = -0.01x + 0.935$) and 95% CI ($R^2 = 0.045$).

Appendix S9.

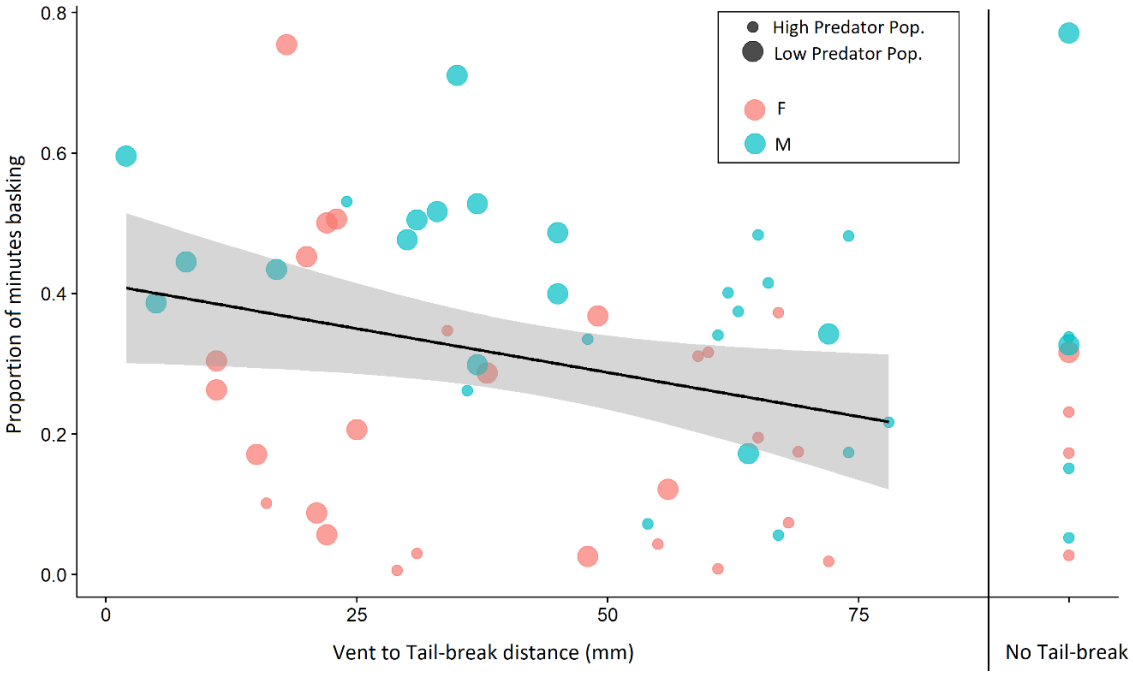

Fig. S9. The non-significant relationship between individual basking frequency (mean across four treatment days) and tail-break severity. More severe tail-breaks are represented by smaller vent to tail-break distances. Plot includes the line of best fit (y = -0.0025x + 0.41) and 95% CI (R^2 = 0.083).

Appendix S10.

Table S10. Summary of the model sets (ΔAICc < 6) for skink basking frequency. Model terms, with reference levels for estimates in italics, were population (*P, high-predator* vs low-predator), treatment (*Tr*, *control*/cat [C]/cat scent [CS]/raptor [R]) and sex (*female*/male), as well as biologically meaningful interactions between these terms and interactions with temperature. Included are the model number (#, refer to Appendix S5), the number of estimated parameters (*K*), the maximum log-likelihood (ln*L*), AICc values, AICc differences (Δ_i), the model weight (*W*), and conditional (R^2c) and marginal (R^2m) values for model fit. Parameter estimates ± SE are included for all models in a given set.

Period	#	*K*	ln*L*	AICc	Δ_i	*W*	R^2c	R^2m	*Intercept*	*P*	*Tr*	*Sex*	*P:Tr*	*Tr:temp*	*temp*
All day	8	14	-1373.2	2776.2	0.00	0.51	0.35	0.18	-3.25 ± 0.36	1.18 ± 0.33	C = 0.06 ± 0.14 S = -0.32 ± 0.14 R = -0.34 ± 0.14	1.08 ± 0.25	-	-	0.23 ± 0.09
	7	13	-1377.0	2781.5	5.39	0.03	0.35	0.12	-2.67 ± 0.44	-	C = 0.07 ± 0.14 S = -0.33 ± 0.14 R = -0.34 ± 0.14	1.08 ± 0.25	-	-	0.24 ± 0.09
Cat exposure	10	17	-845.3	1727.2	0.00	0.54	0.39	0.19	- 3.32 ± 0.47	0.99 ± 0.47	C = -1.01 ± 0.27 S = -0.83 ± 0.27 R = -0.67 ± 0.27	1.14 ± 0.30	C = 0.92 ± 0.36 S = 0.79 ± 0.36 R = 0.39 ± 0.35	-	0.13 ± 0.12
	8	14	-849.3	1728.3	1.11	0.31	0.38	0.19	-3.57 ± 0.46	1.50 ± 0.42	C = -0.52 ± 0.19 S = -0.39 ± 0.19 R = -0.48 ± 0.20	1.14 ± 0.30	-	-	0.12 ± 0.12
	6	11	-854.1	1731.3	4.14	0.07	0.38	0.18	-3.99 ± 0.43	1.50 ± 0.42	-	1.14 ± 0.30	-	-	0.19 ± 0.09
Raptor exposure	10	17	-764.7	1565.9	0.00	0.94	0.61	0.37	-5.15 ± 0.65	1.27 ± 0.62	C = -0.58 ± 0.36 S = 1.29 ± 0.39 R = -2.13± 0.40	1.86 ± 0.46	C = 0.72 ± 0.48 S = 1.96 ± 0.49 R = 1.99 ± 0.51	-	0.16 ± 0.16

Appendix S11.

Table S11. Marginal mean contrasts between treatments for each population (high predator population (HPP) and low predator popultion (LPP) where relevant) based on the top-ranked model for each exposure period. *Italics* indicate treatments that are significantly different from the control. P-values are adjusted using the tukey method for comparing a family of 4 estimates. Tests are performed on the log odds ratio scale.

Period	Population	Contrast	OR	SE	z-ratio	p-value
All Day	Both	ctrl/cat	0.94	0.13	-0.44	0.97
		ctrl/cat scent	1.38	0.20	2.26	0.11
		ctrl/raptor	1.40	0.21	2.22	0.12
Cat exposure	HPP	*ctrl/cat*	*2.76*	*0.74*	*3.79*	*<0.001*
		ctrl/cat scent	*2.29*	*0.63*	*3.02*	*0.01*
		ctrl/raptor	1.95	0.52	2.49	0.06
	LPP	ctrl/cat	1.10	0.27	0.38	0.98
		ctrl/cat scent	1.04	0.25	0.16	1.00
		ctrl/raptor	1.32	0.34	1.07	0.71
Raptor exposure	HPP	ctrl/cat	1.79	0.65	1.61	0.37
		ctrl/cat scent	*3.65*	*1.41*	*3.36*	*<0.01*
		ctrl/raptor	*8.40*	*3.34*	*5.34*	*<0.001*
	LPP	ctrl/cat	0.08	0.29	-0.42	0.98
		ctrl/cat scent	0.51	0.16	-2.08	0.16
		ctrl/raptor	1.15	0.41	0.39	0.98

Appendix S12.

Table S12. Summary of the model sets for basking site preference based on (a) high-refuge vs. low-refuge sites and (b) cat scented vs. control scented sites. Prior to analysis for (a) 'All day' we excluded the daily data for any individual where total basking frequency was in the bottom quartile (individual observed basking on < 50 occasions) for a given treatment day. Prior to analysis for (a) 'Cat exposure' and 'Raptor exposure' we excluded the daily data for individuals where observed basking on < 10 occasions during the relevant exposure period (Symbols as for Appendix S10).

Period	**#**	***K***	**ln*L***	**AICc**	**Δ_i**	***W***	**R^2c**	**R^2m**	***Intercept***	***P***	***Tr***	***Sex***	***P:Tr***	***Tr:temp***	***temp***
(a) High refuge vs. low refuge basking sites															
All day	5	**10**	**-777.7**	**1576.5**	**0.00**	**0.34**	0.20	0.04	**2.18 ± 0.27**	**-0.79 ± 0.26**		-	-	-	-0.07 **± 0.06**
	1	**9**	**-781.1**	**1581.2**	**4.69**	**0.03**	0.20	0.00	**1.73 ± 0.30**	-	-	-	-	-	-0.06 **± 0.06**
Cat exposure	**3**	**7**	**-353.7**	**722.2**	**0.00**	**0.52**	0.25	0.04	**1.29 ± 0.00**	-	C = 1.23 **± 0.00**	-	-	N/A	N/A
											S = 0.93 ± 0.00				
											R = 0.92 **± 0.00**				
Raptor exposure	**2**	5	-341.7	693.9	0.00	0.34	0.22	0.04	**3.21 ± 0.48**	-1.13 **± 0.56**	-	-	-	N/A	N/A
	1	4	-343.2	694.8	0.90	0.22	0.21	0.00	**2.48 ± 0.34**	**-**	-	-	-	N/A	N/A
(b) Cat scented vs. non-scented basking sites															
All day	**3**	12	-1049.7	2124.7	0.00	0.21	0.18	0.01	**0.26** ± 0.27	**-**	C = 0.31 ± 0.16	-	-	-	0.05 ± 0.10
											S = 0.38 ± 0.17				
											R = 0.10 ± 0.18				
	1	9	-1053.2	2125.2	0.50	0.16	0.17	0.01	0.38 ± 0.24	**-**	-	-	-	-	-